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GLEICHENIACEAE SPORES FROM LOWER CRETACEOUS DEPOSITS OF HUNGARY

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Abstract

The present palynological study discusses Gleicheniaceae-type spores isolated from the Lower Cretaceous sediments of Hungary.

Twenty species were identified and placed into the following organgenera as follows:

Gleicheniidites (11 species), *Clavifera* (4 species), *Plicifera* (2 species), and *Ornamentifera* (3 species).

Stratigraphically the Gleicheniaceae spores play an important part in the spore-pollen complexes of the Upper Barremian to Lower Aptian deposits of the Mts Bakony, and Albian sediments of the Mts Villány, where mainly species of the *Gleicheniidites* and *Plicifera* organgenera predominate.

Both the actual number of spores and the number of species decreases for the Gleicheniaceae spores in the Albian assemblages of the Transdanubian Central Mts, but here appear the typical forms of the *Ornamentifera* and *Clavifera* species.

Introduction

The Gleicheniaceae is one of the Filicales order widest known ancient fern families.

The recent Gleicheniaceae species number about 160.

Their zone of distribution ranges from the Korean peninsula and Florida to New Zealand (SEWARD, 1912).

The shoots of recent species usually crawl on the ground or are slightly raised; in the latter instances they climb on shrubs or trees. Their sori are arranged in row, lack indusia, and have few (2—8) sporangia. The spores are trilete or monolete homoiospores.

The Gleicheniaceae ancestral representatives have been traced from the Carboniferous age, but significantly they became widespread only in the Mesozoic. The number of fossil leaf records traced from Jurassic and Cretaceous is large. We can find the tabulated summary of these megafossils in the excellent work of BOLCHOVITINA (1968). The associated and dispersed „gleicheniid” spores of Lower Cretaceous rocks are very similar to modern Gleicheniaceae spores. Shared characteristics of the modern and fossil „gleicheniid” spores are the following:

- triangular equatorial outline;
- interradial crassitudes at the equator;
- presence of arcuate folds on the distal surface;
- usually smooth, rarely ornamented exosporium.

Besides the above, certain fossil forms also have the following characteristics:
 presence of processes or clavate projections at the corners (radial crassitudes);
 a broad equatorial thickening on the distal face (distal crassitudes).

Previous works

COPELAND (1947), NAKAI (1950), HOLTUM (1957) have studied the recent Gleicheniaceae family classification the most extensively. From among them we consider most important the work of NAKAI, who also included the spores' characteristics on the classification. He distinguished three subfamilies: Gleichenioideae and Stromatopterideae have trilete spores, Sticherioideae has monolete spores. From among the Gleicheniaceae spores of the Cretaceous time we know only trilete forms, the classification of which is based on the spore morphology. The most widely known of these works are those of KRUTZSCH (1959), and BOLCHOVITINA (1966, 1968).

The first fossil „gleicheniid“ spore was described by ROSS (1949) as *Gleicheniidites senonicus*, from the Senonian of ÅSEN (Sweden), but he did not give a generic diagnosis. Upon the suggestion of DELCOURT and SPRUMONT (1955) the genus name *Gleicheniidites*, was retained with *Gl. senonicus* as its type species. BOLCHOVITINA (1953), COOKSON (1953), ROUSE (1957), and GRIGORJEVA (1961) described many „gleicheniid“ types and placed the forms into the natural genus *Gleichenia* SMITH. KRUTZSCH (1959) created six subgeneric categories within the *Gleicheniidites* ROSS, on the basis of inter-radial thickenings, the ornamentation, and the projections at the apices. BOLCHOVITINA (1966) divided the *Gleicheniidites* genus into four new organ genera, where the *Clavifera* n. gen. essentially corresponds to the *Gleicheniidites* (*Triplexisporis*) W. KR. 1959 subformgenus, and *Ornamentifera* n. gen. to the *Gleicheniidites* (*Peregrinisporis*) W. KR. 1959 subformgenus.

Bolchovitina's third new genus, *Plicifera*, has three arcuate folds on the distal surface and equatorially uniformly thin walls on the spore.

At the same time she didn't attribute subgenus status to KRUTZSCH's four other subgenera. One can agree with BOLCHOVITINA's opinion since KRUTZSCH designated as the main differences between the *Gleicheniidites* (*Gleicheniidites*), *Gleicheniidites* (*Toridistalisporis*), *Gleicheniidites* (*Radiatisporis*), and *Gleicheniidites* (*Laticrassisporis*) subgenera the deviation in the interrational wall thickenings and the location of the „Tori“ on the proximal or distal surface. From our material it is also apparent that the arcuate folds, referred to by KRUTZSCH as the „Tori“ practically always appear on the distal surface. Although in Middle-European palynological literature KRUTZSCH's nomenclature is becoming widespread, we consider the names created by BOLCHOVITINA more acceptable and follow them in the present work.

SKARBY's (1964) work is very important from the point of view of species diagnosis. Aided by a re-examination of ROSS' (1949) original material, she gave exact genus and species descriptions on the basis of the *Gleicheniidites senonicus* lectotype. Also, by examining and demonstrating disperse and associated spores, collected from the type location, she revised some that were described as other forms, designating them as synonyms of *Gleicheniidites senonicus*. The most important among them are:

- a) *Gleicheniidites circinnidites* COOKSON 1953.

We find many forms published and illustrated with this name in Lower

Cretaceous works, that give a very heterogeneous picture of the species. Most of them resemble *Gl. senonicus* Ross.

However, in our opinion, based on the photograph of COOKSON's type species, it is rather a synonym of *Gleicheniidites umbonatus* (BOLCH. 1953) BOLCH. 1968 than of *Gl. senonicus* Ross 1949.

- b) *Gleichenia stellata* BOLCH. 1953, *Leiotriletes orientalis* BOLCH. 1953, *Gleichenia angulata* BOLCH. 1953 species BOLCHOVITINA (1968) herself admits that SKARBY's photographs convinced her that these forms belong to *Gl. senonicus*. She herself would not write them as individual species in her above works! It is also significant that after 1968 mainly Soviet-work publishes these species names as „gleicheniid“ forms.
- c) *Gleichenia dicarpoides* GRIGORIEVA 1961 is also a synonym of *Gl. senonicus* Ross.
- d) SKARBY (1964) placed the *Gleichenia laeta* BOLCH. 1953, *Gleichenia umbonata* BOLCH. 1953, and *Gleicheniidites (Toridistalisporis) toriconcavus* W. KR. 1959 species in she synonymy. We do not agree with this opinion.

The following works from the Hungarian literature on the Lower Cretaceous are concerned with Gleicheniaceae spores: DEÁK (1963) from the Albian of Mts Bakony, GÓCZÁN (in FÜLÖP, 1966) from the Albian of Mts Villány, RÁKOSI (1972) from the Neocomian of the Basin Dorog, and MIHÁLTZ—FARAGÓ and JUHÁSZ (1972) from recycled sporomorphs of Borehole 11. at Lőkősháza.

Systematic description

Anteturma: SPORITES H. POT. 1893

Turma: TRILETES REINSCH 1881

Subturma: ZONOTRILETES WALTZ 1935

Infraturma: TRICRASSATI DETTMANN 1963

Organ genus: *GLEICHENIIDITES* (Ross 1949) BOLCH. 1968.

Remarks: DETTMANN's (1963), SKARBY's (1964), and BOLCHOVITINA's (1968) diagnoses are very similar. They all contain the characteristics listed below: Triangular, trilete microspores. Smooth or almost smooth exosporium with equatorial thickenings (interradial crassitudes). Usually arcuate folds may be found on the distal surface.

Gleicheniidites senonicus Ross 1949

Pl. I., Figs. 1—4.

1949 *Gleicheniidites senonicus* Ross, p. 31—32. Pl. I. Fig. 3.

Remarks: SKARBY (1964), and BOLCHOVITINA (1968) both publish a synonym list where various authors consider *Gl. senonicus* Ross as synonym of the published species of *Gl. senonicus* or of another species (38 names appear on each list).

Distribution: A widely distributed species in the Lower Cretaceous of Europe and North America. In Hungary it is one of the most abundant forms in the Barremian to Lower Aptian sediments.

Gleichenioidites umbonatus (BOLCH. 1953) BOLCH. 1968
Pl. I., Figs. 5, 6.

1953 *Gleichenia umbonata* BOLCHOVITINA, p. 53, Pl. 8, Figs. 4—7.

1968 *Gleichenioidites umbonatus* (BOLCH. 1953) BOLCHOVITINA, p. 41, Pl. 9., Figs. 1—9.

Description: Amb triangular, apices sharp; the outer margin of the crassitides sinuous, inner wall-contour straight. The interradian crassitides are 3,5—4 μ thick, becoming much thinner at the apices. On the distal face there are narrow, strongly concave folds. Size: 25—33 μ .

Remarks: The description of *Gleichenioidites* (*Tiremisporites*) *bolchovitinae* DÖRING 1965 agrees with that of *Gl. umbonatus* (BOLCH. 1953) BOLCH. 1968, it is a junior synonym of the latter species.

Occurrence: A common species of Sümeg Formation in the Bakony Mts.

Gleichenioidites delcourti DÖRING 1965
Pl. I., Figs. 7, 8.

1965 *Gleichenioidites delcourti* DÖRING, p. 29, Pl. 18, F. 9, 10.

Description: A triangular spore with straight or slightly convex sides, acute corners. The interradian crassitides are well developed, 5—8 μ at centre, exosporium smooth, approximately 1 μ thick near apices. The 3—4 μ thick arcuate folds on the distal surface are so strongly concave that they almost touch each other. Size range: 40—44 μ .

Occurrence: The species is recorded from Wealden of GDR, Belgium and the Netherlands. In Hungary it occurs throughout the Neocomian of the Dorog Basin (RÁKOSI, 1972), and Sümeg Formation of the Bakony Mts (Barremian-Aptian).

Gleichenioidites radiatus (BOLCH. 1953) BOLCH. 1968
Pl. I., Figs. 9, 10.

1953 *Gleichenia radiata* BOLCHOVITINA, p. 54, Pl. 8, Figs. 14, 15.

1968 *Gleichenioidites radiatus* (BOLCHOVITINA 1953) BOLCHOVITINA, p. 43, Pl. 9, Figs. 8—10.

Description: Triangular spore with straight or concave sides and pointed apices. The interradian thickenings are 2—3 μ wide. On the distal surface are three, 3,5—4 μ wide folds on which little stripes, parallel to each other are perpendicularly located. Size range: 28 μ .

Occurrence: A rare form which occurs in the Tés Formation (Middle Albian) of the Bakony Mts, Hungary.

Bolchovitina described this form from Aptian of Russian Platform and from Cenomanian of Middle Urals.

Gleichenioidites rasilis (BOLCH. 1953) BOLCH. 1968
Pl. I., Figs. 11, 12.

1953 *Gleichenia rasilis* BOLCHOVITINA, p. 53, Pl. 7, Figs. 16—18.

1968 *Gleichenioidites rasilis* (BOLCH. 1953) BOLCHOVITINA, p. 43, Pl. 11, Figs. 1—7.

Description: Trilete spore with triangular or rounded triangular amb and rather convex sides. Compared to the spore size it has wide, 3—4 μ , *lens-shaped* inter-radial crassitudes. (This lends to the form the rounded equator contour!). The arcuate distal folds are narrow. Size range: 32 μ .

Occurrence: The species is of widespread geographic and stratigraphic distribution in the USSR. It appears in strata of Albian age in the Transdanubian Central Mts, Hungary.

Gleichenioidites compositus (BOLCH. 1953) DEÁK 1964

Pl. I., Figs. 15, 16.

1953 *Stenozonotrilites compositus* BOLCHOVITINA, p. 46, Pl. 6, F. 8.

1964 *Gleichenioidites compositus* (BOLCH. 1953) DEÁK, p. 97, Pl. 1., Fig. 10.

Description: Triangular form with pointed apices. The outer contour of the equatorial sides is slightly sinuous, the inner contour is almost straight. The distal folds are slightly arcuated, thus the area enclosed by them is relatively large. Size range: 22—28 μ .

Occurrence: Occurs infrequently throughout the Tés Formation (Middle Albian) in Hungary.

Gleichenioidites minor DÖRING 1965

Pl. I., Figs. 13, 14.

1965 *Gleichenioidites* (*Triremisporites*) *minor* DÖRING, p. 28, Pl. 5., Figs. 9—11.

Remarks: The fact that *Gleichenioidites minor* has an interrarial thickening that reaches 7 μ , and that both the inner and outer contours of the spore wall are both sinuous distinguishes it from *Gl. umbonatus* and *Gl. compositus* that possess 3—4 μ and 2—3 μ thick exosporium respectively and sinuous outer, straight inner wall contours.

Occurrence: *Gl. minor* is of widespread distribution in the early Lower Cretaceous sediments: in GDR from Wealdien at Mecklenburg; in USSR from the Neocomian of Basin Donec; in Hungary from the Neocomian of the Dorog Basin, and from the Sümeg Formation.

Gleichenioidites laetus (BOLCH. 1953) BOLCH. 1968

Pl. I., Figs. 17—20.

1953 *Gleichenia laeta* BOLCHOVITINA, p. 22, Pl. 2, Figs. 5—7.

1968 *Gleichenioidites laetus* (BOLCH. 1953) BOLCHOVITINA, p. 40, Pl. 6., Figs. 35—46.

Remarks: The smallest sized Gleicheniaceae species. Spore size: 16—22 μ . It possesses straight or concave sides and triangular amb. The interrarial crassitudes are 1—1,5 μ wide, and may narrow down to 0,5 μ at the corners. The distal folds are very thin and easily wrinkle.

Occurrence: The species is common throughout the Lower Cretaceous of USSR.

GÓCZÁN (1966) recorded a large number from the Albian of Villány Mts; a frequent form in the Vértessomló Formation (Lower Albian) in Hungary.

Gleichenioidites carinatus (BOLCH. 1953) BOLCH. 1968
Pl. I., Figs. 25, 26.

1953 *Gleichenia carinata* BOLCHOVITINA, p. 53, Pl. 7, Figs. 14, 15.

1968 *Gleichenioidites carinatus* (BOLCH. 1953) BOLCHOVITINA, p. 42, Pl. 9, Figs. 1—15.

Description: Subtriangular, rarely rounded amb with straight or convex sides. The trapezoid-shaped interrarial crassitudes are 6—8 μ wide. The distal folds may be as thick as 4—5 μ . Size range: 45—64 μ . (This is the largest sized „gleicheniid“ spore).

Occurrence: USSR: wide geographical and stratigraphical distribution in Lower Cretaceous. In Hungary: a common form from Vértessomló Formation of Gerecse Mts (Lower Albian), and the Tés Formation of the Bakony Mts (Middle Albian).

Gleichenioidites latifolius DÖRING 1965
Pl. II., Figs. 1, 2.

1965 *Gleichenioidites* (*Triremisporites*) *latifolius* DÖRING, p. 30, Pl. 6, Figs. 9, 10.

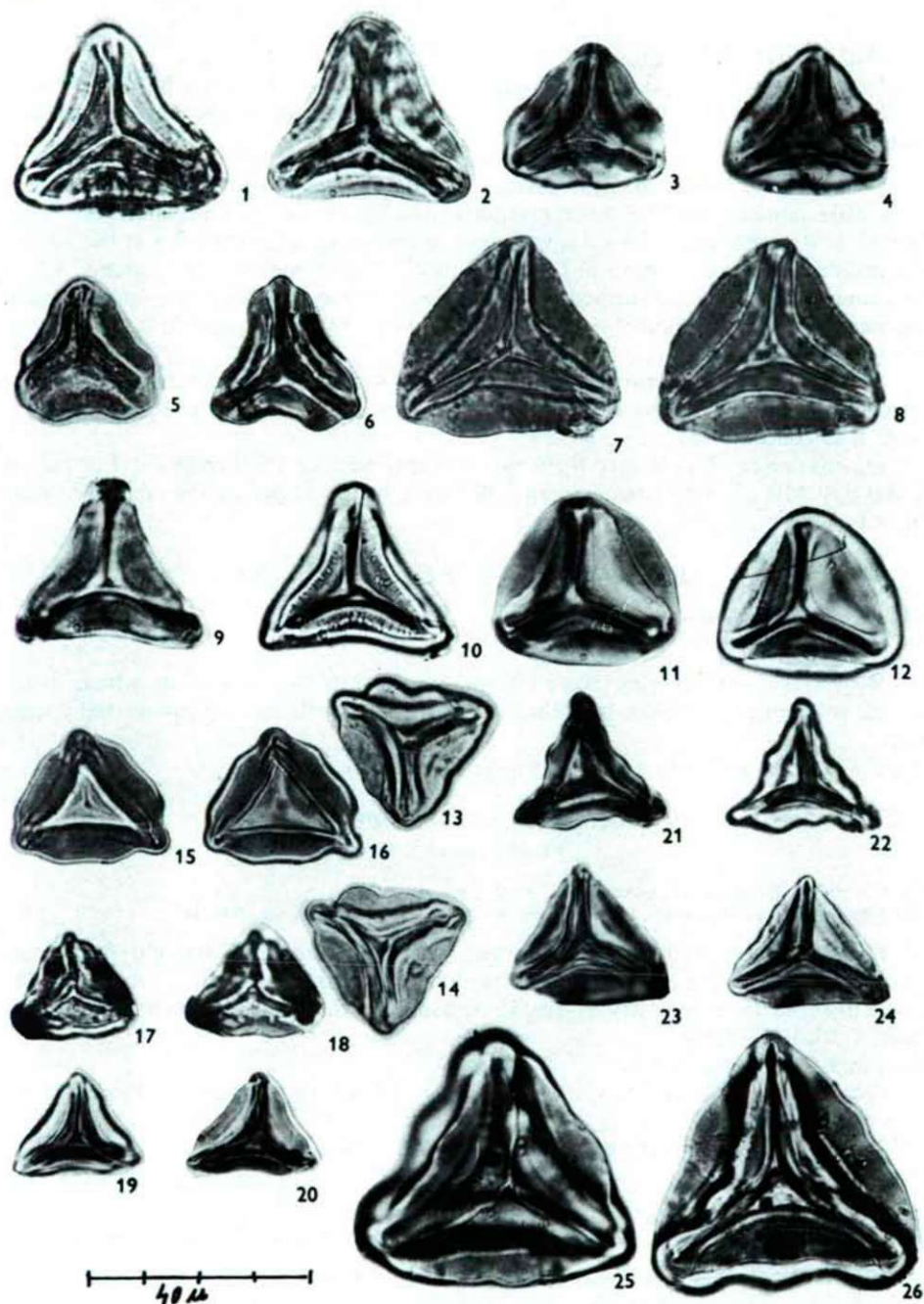
Description: A subtriangular spore form with a strongly concave amb, and corners rounded in a wide arc. The interrarial crassitudes are very wide, 6—8 μ , and narrow down suddenly to 1 μ toward the corners. The three, comparatively thin, 1—1.5 μ wide arcuate folds are on the distal surface. Size range: 37 μ .

Occurrence: Its appearance in the Upper Jurassic—Wealdien rocks at Mecklenburg in GDR is, described by DÖRING (1965). In Hungary it is a rare form which occurs in the Albian and Neocomian sediments of the Transdanubian Central Mts.

Plate I

- 1, 2 *Gleichenioidites senonicus* (ROSS 1949) BOLCH. 1968
Bakony Mts, Sümeg, Süt-17: 202,5. P: 44,7/91,5. Lower Aptian.
- 3, 4 *Gleichenioidites senonicus* (ROSS 1949) BOLCH. 1968
Bakony Mts, Tés. Té-27: 49/2. P: 29/104,4. Middle Albian.
- 5 *Gleichenioidites umbonatus* (BOLCH. 1953) BOLCH. 1968
Gerecse Mts, Bikol. Süttő-3: 125/1. P: 33,6/99,1. Lower Albian.
- 6 *Gleichenioidites umbonatus* (BOLCH. 1953) BOLCH. 1968
Bakony Mts, Sümeg, Süt-17: 332/1. P: 35/98. Upper Barremian.
- 7, 8 *Gleichenioidites delcourti* DÖRING 1965
Bakony Mts, Sümeg. Süt-17: 217,3/1. P: 41,1/92,5. Lower Aptian.
- 9, 10 *Gleichenioidites radiatus* (BOLCH. 1953) BOLCH. 1968
Bakony Mts, Sur. Sur-1: 556,7/1. P: 33,7/109. Middle Albian.
- 11, 12 *Gleichenioidites rasilis* (BOLCH. 1953) BOLCH. 1968.
Bakony Mts, Sur. Sur-1: 556,7/1. P: 38,9/102. Middle Albian.
- 13, 14 *Gleichenioidites minor* DÖRING 1965
Bakony Mts, Devecser. Dv-3: 1288,6/1. P: 41,5/95,5. Barremian.
- 15, 16 *Gleichenioidites compositus* (BOLCH. 1953) DEÁK 1964.
Bakony Mts, Úrkút. Ú-5: 71,2/5. P: 31,6/110,2. Middle Albian.
- 17, 18 *Gleichenioidites laetus* (BOLCH. 1953) BOLCH. 1968.
Gerecse Mts, Bikol. Süttő-3: 125/4. P: 32/104,2. Lower Albian.
- 19, 20 *Gleichenioidites laetus* (BOLCH. 1953) BOLCH. 1968.
Gerecse Mts, Vértessomló. Vst-5: 42/1. P: 44/100. Lower Albian.
- 21, 22 *Clavifera negra* (BOLCH. 1953) n. comb.
Bakony Mts, Úrkút. Ú-5: 71,2/5. P: 31,6/110,4. Middle Albian.
- 23, 24 *Clavifera* cf. *negra* (BOLCH. 1953) n. comb.
Bakony Mts, Úrkút. Ú-5: 73,2/6. P: 37,2/102,6. Middle Albian.
- 25, 26 *Gleichenioidites carinatus* (BOLCH. 1953) BOLCH. 1968.
Gerecse Mts, Bikol. Süttő-3: 90/1. P: 41,5/99,3. Lower Albian.

Plate I



Gleicheniidites saparicus n. sp.

Pl. II., Figs. 3, 4.

Holotype: Pl. II., Figs. 3, 4. Prep.: Sz—42, 80:3/6. P: 38/103.

Locus typicus: Bakony Mts, Szápár. Borehole Sz—42, 115,8 m.

Stratum typicum: Turrillites marl. Upper part of Pénzeskút Formation (Lower Cenomanian).

Diagnosis: Trilete miospore with rounded amb and convex sides. The apices are a little pinched in. The outer margin of the spore wall is undulated, the inner contour is straight. The 3,5—4,5 μ wide interradian crassitudes are 0,7 μ at the apices. The proximal surface is smooth. Laesura simple, slightly sinuous and extends 4/5 of the radius. On the distal surface there are three scarcely arching, 1 μ broad, folds. The part enclosed by them is occasionally decorated by the perisporium remainders. Size range: 34 μ .

Differential diagnosis: The *Gl. saparicus* n. sp. distinct from the other „gleicheniid“ species by its rounded amb, and its sinuous outer and straight inner spore wall contour.

Occurrence: Not a rare form in the upper part of the Pénzeskút Formation of Bakony Mts (Lower Cenomanian). It hasn't occurred yet in the older (Albian) deposits.

Organ genus: *PLICIFERA* BOLCH. 19661966 *Plicifera* BOLCHOVITINA, p. 68.1967 *Plicifera* BOLCHOVITINA, p. 62.

Remarks: *Bolchovitina* placed those forms into this genus on which distal arcuate folds may be found, but which have smooth walls lacking interradian crassitudes.

Type species: *Plicifera delicata* (BOLCH. 1953) BOLCH. 1966.

Plicifera decora (CHLONOVA 1960) BOLCH. 1968

Pl. II., Figs. 5, 6.

1960 *Gleichenia decorus* CHLONOVA, p. 18, Pl. 2, Figs. 4—6.1968 *Plicifera decora* (CHLONOVA 1960) BOLCHOVITINA, p. 36, Pl. 6, Figs. 20—34.

Description: Trilete miospore with triangular amb and straight or slightly concave sides, rounded apices. The exosporium is thin and smooth. The arcuate folds on the distal surface may vary in length, occasionally they may even reach the apices. Their width is 1—1,5 μ .

Size range: 20—26 μ .

Occurrence: A rare form which occurs in the Albian sediments of Bakony Mts.

Plicitera delicata (BOLCH. 1953) BOLCH. 1966

Pl. II., Figs. 7, 8.

1953 *Gleichenia delicata* BOLCHOVITINA, p. 22, Pl. 2, Figs. 1—4.1968. *Plicifera delicata* (BOLCH. 1953) BOLCHOVITINA, p. 35, Pl. 5, Figs. 14—21, and Pl. 6, Figs. 1—19.

Description: A triangular spore with rounded apices, and slightly convex or straight sides. The exosporium smooth, is uniformly thin, 0,5—1 μ thick. On the

distal surface the three folds are strongly arcuate, the ends of the single folds usually reach the apices. Spore size: 30–42 μ .

Remarks: *Bolchovitina* places those forms smaller than 26 μ into *Plicifera decora*, and those larger than 26 μ into *Plicifera delicata*.

Occurrence: A widely distributed species in Lower Cretaceous of USSR. In Hungary a frequent form from Vértessomló Fm. of the Gerecse Mts and Basin Tatabánya.

Organ genus: *ORNAMENTIFERA* BOLCH. 1966

1966 *Ornamentifera* BOLCHOVITINA, p. 69.

1967 *Ornamentifera* BOLCHOVITINA, p. 63.

Remarks: *Bolchovitina* placed those „gleicheniid“ spores here that have inter-radial crassitudes and distal folds, and that also have an ornamented surface. The exosporium may have granulate, tuberculate-verrucate, or echinate ornamentation. This organ genus corresponds to the *Gleicheniidites* (*Peregrinisporis*) W. KR. 1959 subgenus, and to the *Gleicheniidites* GRIGORJEVA 1961 (pars) genus.

The type species: *Ornamentifera echinata* (BOLCH. 1953) BOLCH. 1966

Ornamentifera tuberculata (GRIG. 1961) BOLCH. 1968

Pl. II., Figs. 9, 10.

1961 *Gleicheniidites tuberculatus* GRIGORJEVA, p. 62, Pl. 16, F. 4, 5.

1968 *Ornamentifera tuberculata* (GRIG. 1961) BOLCHOVITINA, p. 51, Pl. 16, Figs. 21–23.

Description: trilete spore with triangular-subtriangular amb, and straight or slightly convex sides, and rounded apices. The 3.5–4 μ wide interrational crassitudes thin down to 2 μ toward the apices. The exosporium is proximally smooth, on the distal surface is finely tuberculate.

The tubercles are very small, being 1 μ high at the maximum. Size range: 39 μ .

Occurrence: Its appearance in the Albian–Cenomanian of West-Siberia, USSR, is described by BOLCHOVITINA (1968).

Occurs infrequently throughout the Tés Formation of Bakony Mts in Hungary (Middle Albian).

Ornamentifera granulata (GRIG. 1961) BOLCH. 1968

Pl. II., Figs. 11, 12.

1961 *Gleicheniidites granulatus* GRIGORJEVA, p. 60, Pl. 15, F. 11–13.

1968 *Ornamentifera granulata* (GRIG. 1961) BOLCHOVITINA, p. 51, Pl. 16, Figs. 5–20.

Description: Trilete spore with a triangular amb, slightly convex sides and rounded apices.

The 2 μ thick exosporium is two-layered. The 1.5 μ thick endexosporium is smooth, the ectexosporium, 0.5 μ thick, is granulate. The interrational crassitude is 4–5 μ wide. On the distal surface the strongly arcuate folds are 2 μ wide. Size range: 38 μ .

Occurrence: It occurs in the Tés Formation of Bakony, Hungary.

Ornamentifera peregrina (BOLCH. 1953) BOLCH. 1968
Pl. II., Figs. 21, 22.

1953 *Gleichenia peregrina* BOLCHOVITINA, p. 55, Pl. 8, Fig. 18.

1968 *Ornamentifera peregrina* (BOLCH. 1953) BOLCHOVITINA, p. 52, Pl. 16, Fig. 24.

Description: Trilete spore with triangular amb, straight or concave sides, and rounded apices. For the spore size its interrational crassitudes are comparatively wide, 4 μ . The distal folds are strongly arcuate and sometimes even touch each other. The exosporium is 1,5 μ thick at the apices. Its entire surface is very densely covered with irregularly shaped, and various sized, around 1 μ , small verrucae. Size range: 26—34 μ .

Occurrence: This species is one of characteristic forms of the upper part of Vértessomló Formation in Mts Gerecse.

Organ genus: *CLAVIFERA* BOLCH. 1966

1966 *Clavifera* BOLCHOVITINA, p. 68.

1967 *Clavifera* BOLCHOVITINA, p. 63.

Remarks: This genus includes those triangular „gleicheniid“ forms that possess interrational crassitudes and distal folds, and which may have apical projections or extension (radial crassitudes), and distal equatorial thickenings (distal crassitudes). The exosporium is smooth or more rarely, tuberculate-verrucate.

Type species: *Clavifera triplex* (BOLCH. 1953) BOLCH. 1966.

Clavifera nigra (BOLCH. 1953) n. comb.
Pl. I., Figs. 21, 22.

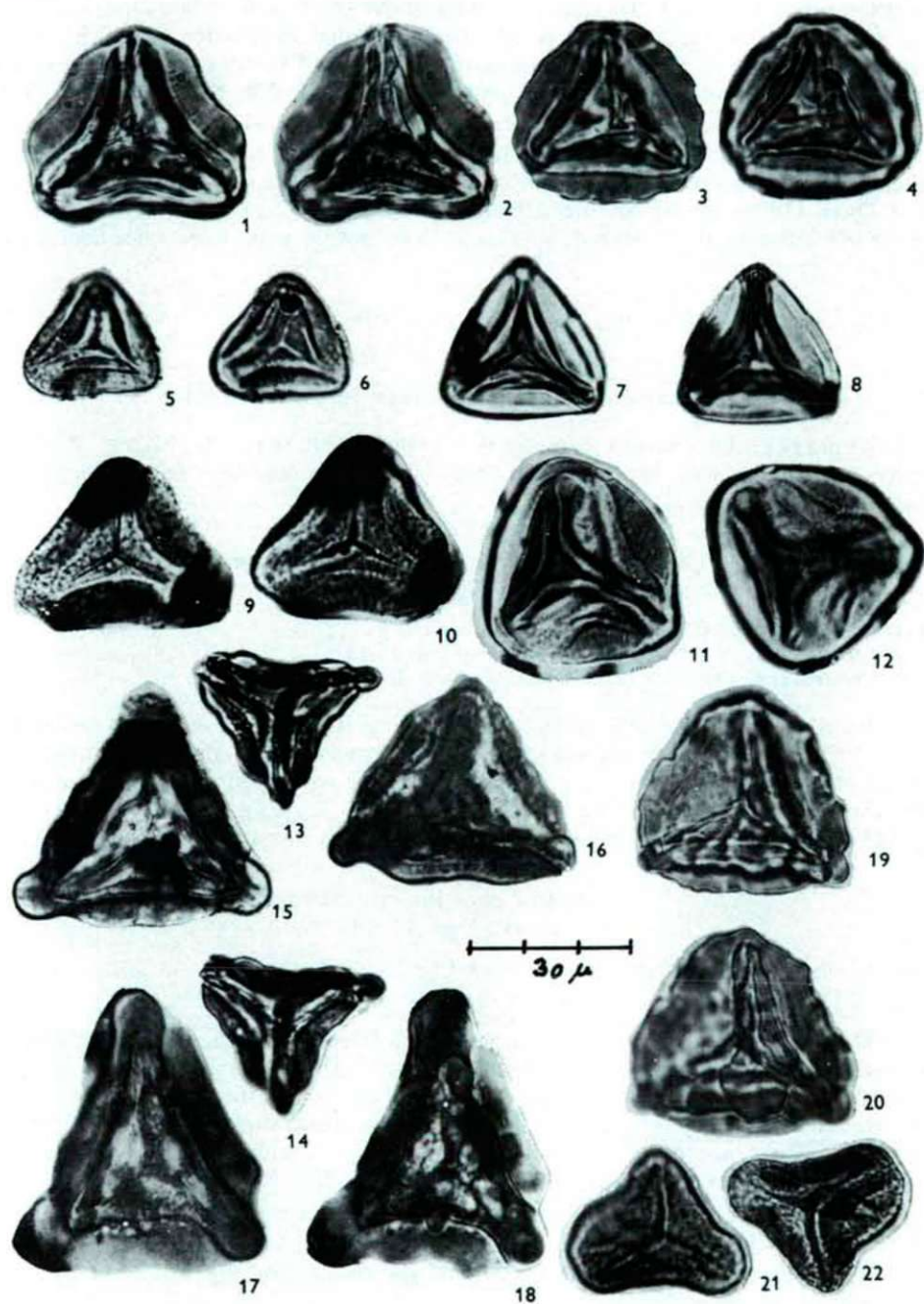
1953 *Gleichenia nigra* BOLCHOVITINA, p. 54, Pl. 8, Figs. 8—9.

1959 *Gleichenioides (Triplexisporis) nigra* (BOLCH. 1953) W. KRUTZSCH, p. 114.

Plate II

- 1, 2s *Gleichenioides latifolius* DÖRING 1965.
Basin Tatabánya. Ta-1329: 461,5/3. P: 43,3/112,1. Lower Albian.
- 3, 4 *Gleichenioides saparicus* n. fsp.
Bakony Mts, Szápár. Sz-42/3/6—1. P: 32/103. Lower Cenomanian.
- 5, 6 *Plicifera decora* (CHLONOVA 1960) BOLCH. 1968
Bakony Mts, Úrkút. Ú-5: 71,2. P: 40,5/95. Middle Albian.
- 7, 8 *Plicifera delicata* (BOLCH. 1953) BOLCH. 1966
Bakony Mts, Sur. Sur-1: 556,7/1. P: 42,4/111. Middle Albian.
- 9, 10 *Ornamentifera tuberculata* (GRIG. 1961) BOLCH. 1968.
Bakony Mts, Sur. Sur-1: 520,9/1. P: 46/90,5. Middle Albian.
- 11, 12 *Ornamentifera granulata* (GRIG. 1961) BOLCH. 1968.
Gerecse Mts, Vértessomló; Vst-5: 72,1/1. P: 39,1/99,4. L. Albian.
- 13, 14 *Clavifera triplex* (BOLCH. 1953) BOLCH. 1966
Bakony Mts, Csehbánya. Cseh-5: 277/1. P: 41,5/108. Middle Albian.
- 15 *Clavifera triplex* (BOLCH. 1953) BOLCH. 1966
Vértessomló, Oroszlány. O-1884: 238/2. P: 42,4/110,9. L. Albian.
- 16 *Clavifera triplex* (BOLCH. 1953) BOLCH. 1966
Bakony Mts, Sümeg. Süt-17: 297,9/1. P: 33/95. Lower Aptian.
- 17, 18 *Clavifera rudis* BOLCH. 1968.
Bakony Mts, Bakonyháza. 2/1—2. P: 40,4/83,9. Upper Albian.
- 19, 20 *Clavifera tuberosa* BOLCH. 1968.
Bakony Mts, Bakonyháza. 2/3—1. P: 32,6/103. Upper Albian.
- 21, 22 *Ornamentifera peregrina* (BOLCH. 1953) BOLCH. 1968.
Gerecse Mts, Bikol. Süttő-3: 104/2. P: 39/103,6. Lower Albian.

Plate II



Description: The spore's amb resembles an equilateral triangle. It has slightly concave sides. The outer and inner contours of the spore wall are sinuous. Laesurae are simple, narrow and reach the apices. The interrational crassitudes, each $2.5\ \mu$ wide, are even and thin down a little bit toward the apices. The distal folds are strongly arcuate; they fuse and take up a large part of the distal surface. Size range: $24\text{--}26\ \mu$.

Remarks: Accepting SKARBY's opinion on the properties of juvenile forms originating from the sporangia of one and the same species, BOLCHOVITINA considers *Clavifera nigra* as an abortive spore of *Gleicheniidites senonicus*. During our study and DEÁK (1964) of the Middle Albian deposits (Tés Formation) in Mts Bakony this form consistently appeared, so that it does not go with other Gleicheniaceae species.

Clavifera cf. *nigra* (BOLCH. 1953) n. comb.
Pl. I., Figs. 23, 24.

1963 cf. *Gleicheniidites circinnidites* (COOKSON 1953) BRENNER, Pl. 11, Figs. 4, 5.

Remarks: This form's contour is a symmetrical triangular shape. With its apices protruding with the aid of the distal folds, it resembles *Clavifera nigra*; its zone of occurrence is also the same.

Clavifera triplex (BOLCH. 1953) BOLCH. 1966
Pl. II., Figs. 13—16.

1953 *Gleichenia triplex* BOLCHOVITINA, p. 55, Pl. 8, Figs. 10—13.

1959 *Gleicheniidites (Triplexisporis) triplex* KRUTZSCH, p. 114.

1968 *Clavifera triplex* (BOLCH. 1953) BOLCHOVITINA, p. 46—47. Pl. 11, 12.

Remarks: A wide geographic distribution of the Lower Cretaceous bears this spore form; it is a well known, well characterized species. Although it occurs in several strata of the Lower Cretaceous, it is dominant in the Aptian-Albian deposits all over the world; the same is also true in Hungary. Its size: $32\text{--}54\ \mu$. The form and size of radial crassitudes may vary greatly. The spore is smooth with straight or sinuous sides.

Clavifera rudis BOLCH. 1968
Pl. II., Figs. 17, 18.

1968 *Clavifera rudis* BOLCHOVITINA, p. 48, Pl. 13, Figs. 9—18, Pl. 14, Figs. 1—15, and Pl. 15, Figs. 1—12.

Description: This is a large spore with a triangular amb, straight or slightly convex sides and knobby extensions on the apices. The proximal surface is smooth and sharply distinguished from the equatorial part where there is a wide, $7\text{--}9\ \mu$, interrational thickening. The central portion of the distal surface is sculptured with verrucae. These are possible: rarely spaced, large, irregular verrucae, or densely distributed, high or short warts (distal crassitudes). Size range: $52\text{--}76\ \mu$.

Occurrence: This species enters the Russian Lower Cretaceous succession in the Aptian (at Harkow).

Its appearance is in the Upper Albian age (Pénzeskút Formation of the Mts Bakony) of Hungary.

Clavifera tuberosa BOLCH. 1968

Pl. II., Figs. 19, 20.

1968 *Clavifera tuberosa* BOLCHOVITINA, p. 47, Pl. 12, Figs. 21—24, Pl. 13, Figs. 1—8.

Description: A triangular spore with straight or slightly convex sides. The laesurae are simple and reach the apices. The extensions on the apices (radial crassitides) do not protrude much. The proximal surface is smooth. On the distal surface there are large tuberculae (distal crassitides), that are somewhat raised from the surface, and that run together. The interradiat thickening is wide, 6—8 μ . On certain specimens distal, arcuate folds may be also appear under the tuberculae. Size range: 36—54 μ .

Occurrence: This species is described by BOLCHOVITINA from the Aptian deposits of Donets Basin and Volgograd, USSR. In Hungary it appears in the Upper Vraconian deposits (Pénzeskút Fm.) of Bakony Mts.

Remarks: On the last two forms recorded by BOLCHOVITINA (1968) the distal surface ornamentation is not typical of *Clavifera*, and much resembles that of the *Trubasporites Vavrdova* genus into which DÖRING (1965) also already placed the verrucate surfaced forms. Here, however, the proximal surface is also richly ornamented, while in *Clavifera rudis*, *Cl. tuberosa*, and *Cl. crassiuscula* the proximal surface is smooth.

Discussion

A series of examinations of the well developed Hungarian Lower Cretaceous deposits, thus Barremian-Aptian (Sümege Formation) of Bakony, Albian-Lower Cenomanian (Tés Formation and Pénzeskút Formation) of Mts Bakony and Vértes, the Neocomian and Lower Albian (Vértessomló Formation) of Mts Gerecse, as well as the Albian rocks of Mts Villány have produced a rich collection of Gleicheniaceae spores. We separated twenty species during the study, as the systematic part shows. From among them we placed 11 species into the *Gleichenioidites* genus, 4 species into the *Clavifera*, 3 species into the *Ornamentifera*, and 2 species into the *Plicifera* genus.

The distribution percentage of the Gleicheniaceae spore species in the various aged Lower Cretaceous sediments has stratigraphical importance; that is to say, after the Schizaeales, the Gleicheniaceae family was the most powerful plant group in the Lower Cretaceous.

The probable center of origin and emigration of the Gleicheniaceae was what is now the Russian Platform. Here the number of Gleicheniaceae spores comprised 60—80% of the total spore-pollen complex in the time of the Barremian-Aptian strata. The closeness of this area is also reflected in our spore picture.

In the Barremian age their percentage composition increases by degrees; we can date their time of flowering from the Lower Aptian deposits of the Mts Bakony, where they constitute 45—55% of the spore-pollen complex, and their species number increases. The following species are characteristic of the Barremian:

Gleichenioidites senonicus, *Gl. delcourtii*, *Gl. umbonatus*, *Gl. minor*, and *Gl. laetus*.

In addition to the above *Plicifera delicata*, *Clavifera triplex*, *Gl. carinatus*, and *Gl. rasilis* appear in the Aptian age.

The importance of Gleicheniaceae suddenly diminishes in the Albian deposits. Only in the mid-Albian rocks of the Mts Villány and Mts Bakony we find some accidental enrichment. Representatives of *Gl. senonicus*, *Gl. laetus*, and *Gl. umbonatus* also form the species' bulk here; the other species only rarely occur. However new forms appear that just occasionally occurred in the older deposits or that did not appear at all; such forms in the Lower Albian are *Ornamentifera peregrina*, *Plicifera decora*, *Gleichenioides latifolius*, and in the Middle Albian rocks *Gl. radiatus*, *Gl. compositus*, *Clavifera nigra*, *Clavifera tuberosa*, *Ornamentifera tuberculata*.

In the Upper Albian the mid-Albian forms dominate in addition to *Gl. senonicus* and *Gl. laetus*.

New forms are *Clavifera rudis* and *Ornamentifera granulata*. Furthermore, a characteristic new species of the Lower Cenomanian is *Gleichenioides saparicus* n. sp. Here, however, members of Gleicheniaceae are very rarely present.

The percentage proportion of the various Gleicheniaceae spores in the Barremian and Aptian deserves more detailed attention, however the Albian does not; here the presence or absence of an individual characteristic form can give information together with the other spore types.

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MONOLETE SPORES OF SCHIZAEACEAE FROM HUNGARIAN ALBIAN DEPOSITS

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Abstract

The author studied monolete spores with striate, foveolate, foveo-reticulate and verrucate sculpture coming from Albian deposits of the Transdanubian Central Mountains. Among the 13 species separated out were seven *Corniculatisporites* sp., four *Microfoveolatosporis* sp., one *Cicatricosporites* sp., and one *Verrucatosporites* species representatives. Three new *Microfoveolatosporis* species are proposed, and four new name combinations are suggested.

All of the examined spores fell into the family Schizaeaceae of the Schizaeales order. It may be supposed that the Schizaeaceae family, with monolete spores, continually differentiated as an independent group from the species belonging to the more ancient, trilete spored Schizaeales during the Lower Cretaceous.

Introduction

A striking characteristic in the examination series of Hungarian Lower Cretaceous deposits is the dominance of fern spores. Among them the well ornamented, trilete Schizaeales forms play a prominent part. The monolete spores with striate, foveolate, foveo-reticulate and verrucate ornamentation, occur mainly in the Albian stage. The object of this examination is to find out to which species the monolete spores belong and on the basis of their probable relationship to modern fern species, to which fern family they belong.

Previous works

Several author (BOLCHOVITINA, 1961; POCKOCK, 1964) have established that the striate spores of the Lower Cretaceous are related to those fern species belonging to the Schizaeales order that have striate spores.

According to one classification system the living genera *Anemia*, *Lygodium*, *Mohria* and *Schizaea* are placed into the Schizaeaceae family of Filicales order. Others raise the Schizaeaceae to the rank of Schizaeales. Thus REED (1947), for example, divided the Schizaeales order into the four following families on the basis of the leaf and spore morphology:

1. Schizaeaceae (KAULF.) PRESL;
2. Anemiaceae (PRESL) REED;
3. Lygodiaceae PRESL;
4. Mohriaceae (PRESL) REED.

On the basis of her examination of recent and fossil spores, BOLCHOVITINA (1961) also accepts this classification. MARÓTI (1965) completed a histological examination of the leaves of recent Schizaeales. Because of their great similarity, MARÓTI groups the *Mohria* and *Anemia* genera together under the name of Ornithopteridaceae (BERNH.) MARÓTI; he accepts the Lygodiaceae PRESL. and the Schizaeaceae (KAULF.) PRESL family statuses.

We examined the spores of recent Schizaeaceae species and found the following characteristics:

1. the spores are bean-shaped, bilaterally symmetrical, and monolete;
2. the exosporium of spores is variously sculptured:
 - a) laevigate: *Schizaea poeppigiana* STURM,
Sch. fluminensis STURM,
Sch. sprucei HOOK,
Sch. biroi RICHT.
 - b) striate: *Actinostachys digitata* (L.) WALL.,
A. laevigata (METT.) REED
A. melanesica (SELL.) REED.
 - c) verrucate-tuberculate:
Schizaea incurvata SCH.,
Sch. bifida WILLD.,
Microschizaea tenella (KAULF.) REED.
 - d) foveate-foveolate:
Schizaea pectinata (L.) SW.,
Microschizaea pusilla PURSH.
 - e) granulate: *Schizaea elegans* (VAHL) SW.,
Sch. pectinata (L.) SM.

We also find these sculpture forms in the publications concerned with Mesozoic monolete spores, as in SELLING (1944), KRUTZSCH (1959), BOLCHOVITINA (1961), SRIVASTAVA (1971), and KUYAEVA (1972, 1973).

Their works serve as the basis for the supposition that a part of the monolete spores from the Transdanubian Central Mts (Albian) belong to fossil representatives of the Schizaeaceae family.

Systematic description

Turma: MONOLETES IBRAHIM 1933

Suprasubturma: *Acavatomonoletes* DETTMANN 1963

Subturma: AZONOMONOLETES Lubert 1938

Infraturma: *Ornati* R. POT. 1956

Genus: *CORNICULATISPORITES* KUYAEVA 1972

Welwitschiapites BOLCH. 1953, p. 61.

Welwitschiapites BOLCH. ex POT. 1958, p. 123.

Welwitschiapites BOLCH. ex R. POT. (in DEÁK, 1963)

Type species: *Corniculatisporites magniolobatus* (BOLCH. 1953) KUYAEVA 1972

1953 *Welwitschiapites magniolobatus* BOLCHOVITINA (pars).

Pl. 19, Fig. 19 (non 18). South-Urals, Albian-Cenomanian.

Diagnosis: Monolete, bilaterally symmetrical spores, polarly oval or bobbin-shaped, equatorially bean-shaped; spore body with protrusions at the two longitudinal axes. The thick exosporium is ribbed.

Remarks: BOLCHOVITINA (1953) described and indicated this species as *Welwitschiapites magniolobatus*. Its figure shows two forms that are morphologically unlike. Some authors keep on record the hitherto described *Welwitschiapites* form species -on the basis of a true resemblance to the pollen of the recent *Welwitschia mirabilis* HOOK — as pollen, and suppose they are relatives of *Welwitschia*. In our opinion KUYAEVA (1972) properly recognized that these forms are spores and transferred *Welwitschiapites magniolobatus* to her new spore genus *Corniculatisporites*, as a type species of the genus.

Corniculatisporites virgatus (DEÁK 1963) KUYAEVA 1972

Pl. I., Figs. 1, 2.

1963 *Welwitschiapites virgatus* DEÁK, p. 408, Pl. I., Figs. 1, 2.

Remarks: Large, richly ribbed form. The spore body is sculptured by 2—2.5 μ wide muri, which end by ones or twos in the irregularly conical shaped protrusions at the two ends of the longitudinal axis. Muri number: 26—28. Protrusions 7—9 μ long and 11—13 μ wide. Size range: 76 \times 52 μ .

Occurrence: A rare form which occurs from the Tés Formation (Middle Albian) and Pénezskút Formation (Upper Albian) in the Mts Bakony and Mts Vértes.

Corniculatisporites alekhinii (BOLCH. 1953) KUYAEVA 1972

Pl. I., Figs. 3, 4.

1953 *Welwitschiapites alekhinii* BOLCHOVITINA, p. 61, Pl. 9, F. 20.

1972 *Corniculatisporites alekhinii* (BOLCH. 1953) KUYAEVA, p. 7, Pl. I, Figs. 5—7.

Remarks: A monolete spore ornamented by 12 (5—7 μ wide) muri, which running parallel to each other and to the laesura and fuse by threes into the protrusions at the two longitudinal ends.

Occurrence: The species was described from Campanian strata of the northern Urals (BOLCHOVITINA, 1953), from the Upper Albian of Crimea (KUYAEVA, 1972) in USSR, and from the Aptian of Wienerwald (ČORNA, 1972) in Austria.

In Hungary this species first appears in strata of Lower Albian (Vértessomló Formation), ranges into the Albian, but is common only in the Upper Vraconian sediments of the Mts Bakony.

Corniculatisporites tudariensis KUYAEVA 1972

Pl. I., Figs. 5, 6.

1972 *Corniculatisporites tudariensis* KUYAEVA, p. 9. Pl. I, F. 8—10.

Remarks: the species containing the smallest *Corniculatisporites* forms. The $36 \times 22 \mu$ large spore body is ornamented by 16 muri which fuse to the protrusions by fours.

Occurrence: KUVAEVA recorded it from Cenomanian deposits of the Caucasus, USSR.

Occurs infrequently in the Pénzeskút Formation (Upper Albian) of Mts Bakony.

Corniculatisporites magniobatus (BOLCH. 1953) KUVAEVA 1972

Pl. I., Figs. 7, 8.

1953 *Welwitschiapites magniobatus* BOLCHOVITINA, p. 61, Pl. 9., Fig. 19 (non 18).

1972 *Corniculatisporites magniobatus* (BOLCH. 1953) KUVAEVA, p. 6, Pl. I, Figs. 1—4.

Remarks: On the spore body there are 20 muri parallel to each other. They are $2.5\text{--}3 \mu$ wide, and fuse by twos or rarely threes into the short but wide extensions at the two ends of the long axis. (Among the *Corniculatisporites* species this extension is the shortest.) Size range: 57μ .

Occurrence. BOLCHOVITINA (1953) described it from the Cenomanian of Caucasus; KUVAEVA (1972) recorded it from the Upper Albian of Crimea. This species enters the Hungarian mid-Cretaceous succession to present knowledge, in the Lower Albian (Vértessomló Fm) of the Mts Gerecse.

Corniculatisporites bolchovitinae KUVAEVA 1972

Pl. I., Figs. 9, 10.

1972 *Corniculatisporites bolchovitinae* KUVAEVA, p. 11, Pl. I, F. 14—16.

Remarks: attached to the ends of the spore body of this $56 \times 23 \mu$ large form, — that is somewhat smaller than the holotype, — are comparatively long ($12\text{--}14 \mu$) cylindrical, pointed protrusions. The spore surface is covered by parallelly running, and at places crosswise running, $2\text{--}2.5 \mu$ thick muri. The muri number is $16\text{--}18$. The muri reach by ones to $3/4$ of the length of the protrusions.

Occurrence: The holotype was described from Cenomanian rocks of the Caucasus (KUVAEVA, 1972), in USSR.

Its appearance in the Vértessomló Formation of the Mts Gerecse is common.

Plate I

- 1, 2 *Corniculatisporites virgatus* (DEÁK 1963) KUVAEVA 1972.
Mts Bakony, Balinka. Ba-237: 95/3. P: 46,5/112,1. U. Albian.
- 3, 4 *Corniculatisporites alekhinii* (BOLCH. 1953) KUVAEVA 1972.
Mts Bakony, Balinka. Ba-237: 54/2. P: 32/93. Upper Albian.
- 5, 6 *Corniculatisporites tudariensis* KUVAEVA 1972.
Mts Bakony, Pénzeskút: 5/2. P: 34,5/105. Upper Albian.
- 7, 8 *Corniculatisporites magniobatus* (BOLCH. 1953) KUV. 1972.
Basin Tatabánya, Ta-1369: 317/2. P: 33,5/113,5. Lower Albian.
- 9, 10 *Corniculatisporites bolchovitinae* KUVAEVA 1972.
Mts Gerecse, Bikol. Süttő-3: 125/4. P: 31,2/103,5. L. Albian.
- 11, 12 *Corniculatisporites auritus* (SINGH 1971) n. comb.
Basin Tatabánya, Ta-1329: 695/6. P: 35,5/103,5. Lower Albian.
- 13, 14 *Corniculatisporites nemanicensis* (PAČTOVÁ 1961) n. comb.
Mts Bakony, Hárskút. Hk-4: 641/3. P: 33,5/95,9. Upper Albian.

Plate I



Corniculatisporites auritus (SINGH 1971) n. comb.
Pl. I., Figs. 11, 12.

1971 *Cicatricosporites auritus* SINGH, p. 81, Pl. 10, Figs. 11—15.

Remarks: On the monolete form that SINGH (1971) described 6—8 μ long protrusions may be found at the two ends of the longitudinal axis. The spore is ornamented by 1—2 μ wide muri which continue onto the auriculate protrusions to coalesce with one another at a point; that is the reason for transferring this form into the *Corniculatisporites* genus. The specimen reported by us is somewhat smaller than the holotype. The holotype is 66 \times 35 μ , and our specimen is 53 \times 33 μ . The protrusions are also proportionately smaller.

Occurrence: Its appearance in the Loon River Fm. and Shaftesbury Fm. of the Peace River area, Canada, is described by SINGH (1971). In Hungary it occurs infrequently throughout the Vértessomló Formation (Lower Albian) of the Basin Tatabánya.

Corniculatisporites nemanicensis (PACLTOVÁ 1961) n. comb.
Pl. I., Figs. 13, 14.

1961 *Ephedripites nemanicensis* PACLTOVÁ, p. 63, Pl. 9, Figs. 1—3.

Remarks: A monolete spore with a polarly elliptical amb, and ornamented by thick ribs. The ribs running parallel to each other and to the laesura, fuse by threes to the 6—8 μ long, 5—6 μ wide protrusions at the two longitudinal ends. Ribs 5—6 μ are spaced apart 1 μ , and they are 12 in number. Size range: 76 \times 38 μ .

Occurrence: PACLTOVÁ (1961) recorded it from the Senonian of Nemanice, Czechoslovakia.

A rare form which occurs in the lower part of Pénzeskút Formation (Upper Albian) of the Mts Bakony.

Genus: *CICATRICOSOSPORITES* (TH. PF. 1953) W. KR. 1959

Type species: *Cicatricosporites pseudodorogensis* (TH. & PF. 1953) W. KR. 1959.

W. KRUTZSCH (1959) placed the monolete, cicatricose-canaliculate sculptured forms into this genus, distinguishing them from the similarly ornamented alete forms which are representatives of the *Schizaeoisporites* genus.

Cicatricosporites phaseolus (DELCOURT & SPRUMONT 1955) W. KR. 1959
Pl. II., Figs. 1, 2.

1955 *Schizaeoisporites phaseolus* DELCOURT & SPRUMONT, p. 46, Fig. 13.

1959 *Cicatricosporites phaseolus* (DEL. & SPR. 1955) KRUTZSCH, p. 223.

Remarks: The spore examined by us has a 3—3.5 μ thick exosporium on which muri run obliquely across the spore body and attach parallelly toward the laesura. The muri are 2 μ wide, apart 0.5 μ . Laesura is 25 μ long. Size range: 52 \times 35 μ .

Occurrence: The species is widely distributed in the Albian-Cenomanian deposits of North America and Europa. In Hungary it occurs in the mid-Albian rocks of the Tés Formation, Mts Bakony.

Genus: *VERRUCATOSPORITES* (TH.&PF. 1953) W. KR. 1959

Type species: *Verrucatosporites alienus* (R. POT. 1931c) TH.&PF. 1953.

Verrucatosporites contractus (BOLCH. 1953) W. KR. 1959

Pl. II., Figs. 3, 4.

1953 *Aspidium contractum* BOLCHOVITINA, p. 57, Pl. 9, Figs. 6, 7.

1959 *Verrucatosporites contractus* (BOLCH. 1953) KRUTZSCH, p. 205

Remarks: This monolete spore which is bean-shaped polarly, is sculptured by 3—4 μ high, 3—4.5 μ broad at the base conical formed verrucae that are some places more rare and other places more dense in their distribution. Around the 34 μ long laesura the verrucae are smaller, or may be lacking. Size range: 52 \times 38 μ . (Somewhat larger than the holotype.)

Occurrence: BOLCHOVITINA described it from the Upper Albian of the Southern Urals, USSR. Present in the majority of Vértessomló Formation in the Basin Tatabánya, Oroszlány, Hungary.

Genus: *MICROFOVEOLATOSPORIS* (W. KR. 1959) R. POT. 1966

Type species: *Microfoveolatosporis pseudodentatus* W. KR. 1959

This genus includes monolete spores with foveolate-foveoreticulate ornamentation on the basis of POTONÉ's emendation. He places the *Reticulosporis*, also created by KRUTZSCH, here as the two genera are very similar morphologically.

Microfoveolatosporis baconicus n. sp.

Pl. II., Figs. 5—7.

Holotype: Plate II., Figs. 5, 6. Prep.: Pe—31, 161/1:32,2/102,3.

Locus typicus: Bakony Mts, Olaszfalu. Borehole Pe—31.

Stratum typicum: Pénzeskút Fm., Turrillites marl (Upper Albian)

Diagnosis: monolete, bilaterally symmetrical spore with convex to concave amb. The straight, simple laesura reach to 2/3 of the spore length. The exosporium is 1 μ thick with finely granulate or rarely chagrenate ornamentation on the surface. Among the granulae may be found irregularly placed foveolae. Its maximum diameter 0.5 μ . Size range: 48—55 \times 22—24 μ .

Differential diagnosis: The *M. baconicus* n. sp. can be distinguished from the other *Microfoveolatosporis* species by its sparse, scattered, small foveolae and by its finely granulate surface.

Occurrence: A frequent form in the Bakony Mts and Vértés Mts, from Tés Formation and Pénzeskút Formation (Middle and Upper Albian).

Microfoveolatosporis surensis n. sp.

Pl. II., Figs. 8—11.

Holotype: Plate II., Figs. 10, 11. Prep.: Sur—1, 498,3/3:36,7/90.

Locus typicus: Bakony Mts, Súr. Borehole Súr—1.

Stratum typicum: Tés Formation, clayey-marl (Middle Albian).

Diagnosis: monolete, bilaterally symmetrical spore with concave-convex amb. The simple laesura is bordered by a thin lips, and may be as long as 4/5 of the length of the long axis. The 1—1.5 μ thick exosporium has a rugulate surface. The rugulae

are shaped like crooked sticks, and are about $1\ \mu$ high, and $2-4\ \mu$ long. They form an irregular reticulum that contains $0.5-1\ \mu$ diameter foveolae at a medium density. Size range: $45-66 \times 25-45\ \mu$ (Holotype: $66 \times 45\ \mu$).

Differential diagnosis: The *M. surensis* n. sp. distinct from *Microfoveolatosporis baconicus* n. sp. by the presence of rugulae and among them the occurrence of larger and more densely spaced foveolae.

Remarks: The individual specimens of *M. surensis* n. sp. show large variations in form and size. On the form illustrated in Pl. II. Figs. 8, 9. the ornamentation is finer.

Occurrence: First appears in strata of Middle Albian clayey marl of Tés Formation in the Bakony Mts and is unknown from sediments younger than the lower part of Upper Albian.

Microfoveolatosporis gallicus (DEÁK&COMBAZ 1967) n. comb.

Pl. II., Figs. 12—14.

1967 *Reticulosporis gallicus* DEÁK&COMBAZ, p. 80, Pl. 1, Fig. 22.

Remarks: Monolet spore, with straight laesura which reach $3/4$ the length of the long axis. The two-layered exosporium is $1.5-2\ \mu$ thick; the ect-exosporium is densely perforated with foveolae that are $0.2\ \mu$ in diameter, and the endosporium is covered with $1.5\ \mu$ thick larger pitted and more sparsely spaced foveolae. Thus under high focus the spore surface appears to be foveo-reticulate, with pentagonal reticulae surrounded by $4-5$ foveolae. Size range: $52-65 \times 28-38\ \mu$.

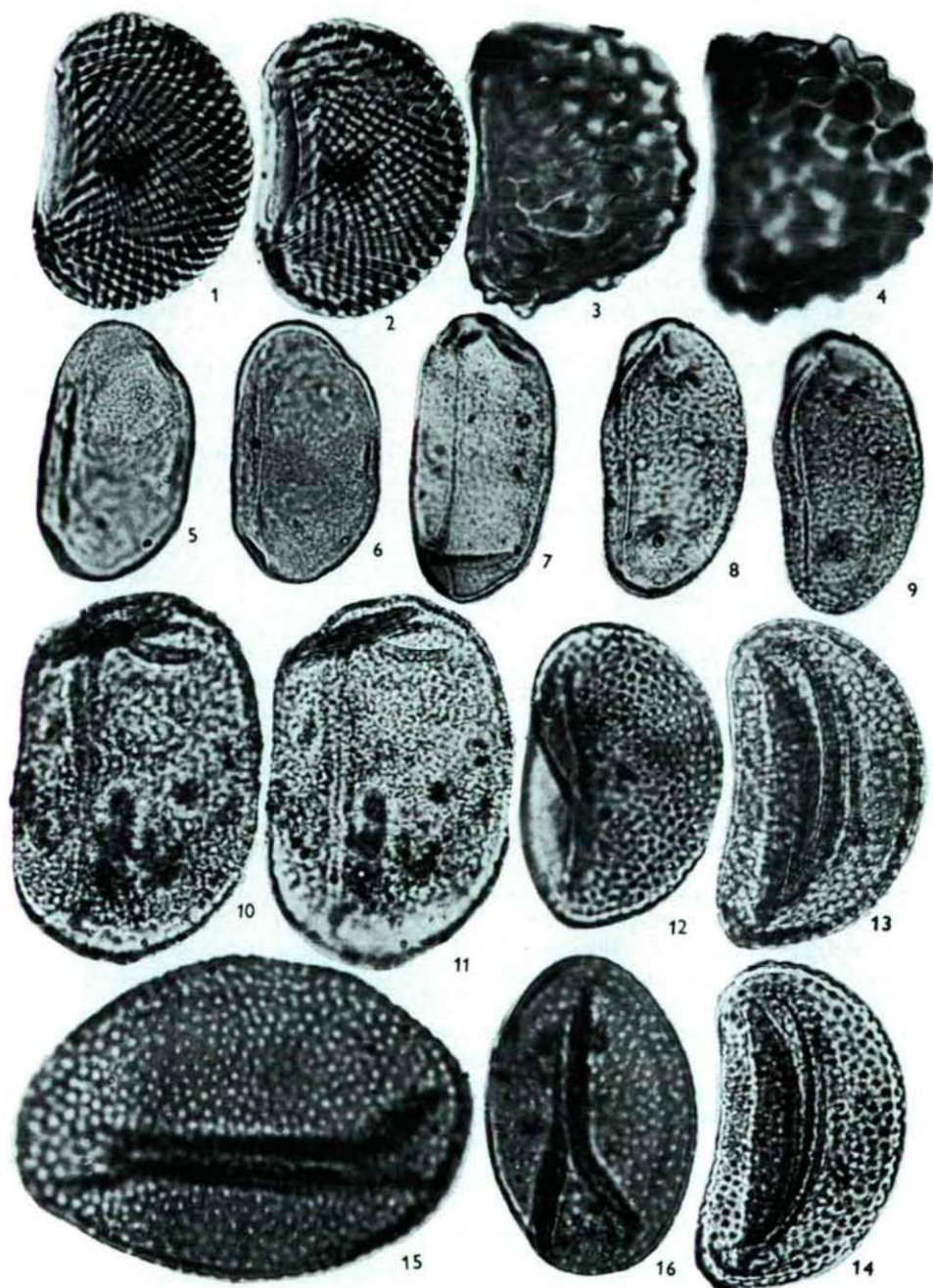
Occurrence: It has been reported from Albian-Cenomanian of Saintogne, France by DEÁK&COMBAZ (1967).

Of infrequent occurrence in certain horizons of the Tés Fm. in Bakony and Vértes Mts.

Plate II

- 1, 2 *Cicatricosporites phaseolus* (DEL.&SPR. 1955) W. KR. 1959.
Mts Bakony, Sur. Sur-1: 556,7/2. P: 35,5/103,3. Middle Albian.
- 3, 4 *Verrucatosporites contractus* (BOLCH. 1953) W. KR. 1959.
Mts Vértes, Oroszlány. O-1884: 217/1. P: 43,1/104. Lower Albian.
- 5—7 *Microfoveolatosporis baconicus* n. fsp.
5, 6: Mts Bakony, Olaszfalu. Pe-31: 161/1. P: 32,2/102,3 U. Alb.
7: Mts Bakony, Sur. Sur-1: 358,5/1. P: 37,3/106,9. M. Albian.
- 8, 9 *Microfoveolatosporis surensis* n. fsp.
Mts Bakony, Sur. Sur-1: 358,5/1. P: 31,9/108,7. Middle Albian.
- 10, 11 *Microfoveolatosporis surensis* n. fsp. Holotypus.
Mts Bakony, Sur. Sur-1: 498,3/1. P: 36,7/90. Middle Albian.
- 12 *Microfoveolatosporis gallicus* (DEÁK&COMBAZ 1967) n. comb.
Mts Vértes, Oroszlány. O-1891: 578/1. P: 39,6/108. Middle Albian.
- 13, 14 *Microfoveolatosporis gallicus* (DEÁK&COMBAZ 1967) n. comb.
Mts Bakony, Sur. Sur-1: 556,7/2. P: 42,9/4,4. Middle Albian.
- 15 *Microfoveolatosporis csaszari* n. fsp. Holotypus
Mts Bakony, Sur-1: 533/1. P: 32/110,8. Middle Albian.
- 16 *Microfoveolatosporis csaszari* n. fsp.
Mts Vértes, Oroszlány. Ot-83: 23,3/1. P: 42,5/105. Middle Albian.

Plate II



Microfoveolatosporis csaszari n. sp.

Pl. II., Figs. 15, 16.

Derivatio nominis: In honor of GÉZA CSÁSZÁR, a Hungarian geologist.

HOLOTYPE: Plate II., Fig. 15. Prep.: Súr—1,533 (l. P: 32) 110,8.

Locus typicus: Bakony Mts, Súr. Borehole Súr—1, 533,3 m.

Stratum typicum: Tés Formation, clayey-marl, Middle Albian.

DIAGNOSIS: equatorially bean-shaped, monolete spore. The laesura asymmetrically follow the long axis, reaching to about 2/3 of it. On most examples the laesura is bounded on two sides by a „labrum“ which separates from the laesura as it approaches the poles. The 1—1,2 μ thick exosporium is one-layered. Foveolae extend into the exosporium. Regularly distributed over the spore surface, they are formed as half-sphaerical dents that are 0,5 μ in diameter. Size range: 60—80 \times 40—58 μ .

Differential diagnosis: The *M. csaszari* n. sp. distinct from *Microfoveolatosporis skottsbergii* (SELLING 1944) SRIVASTAVA 1971 by its smaller size and by the fewer foveolae on its surface; from *Microfoveolatosporis gallicus* (DEÁK&COMBAZ 1967) n. comb. by its one-layered exosporium with its regularly distributed, uniform-sized foveolae; and from *Microfoveolatosporis canaliculatus* DETTMANN 1963 by its larger size and by its foveolae of uniform diameter.

Discussion

We examined the monolete spores occurring in the spore-pollen complexes from the palynological examination series on the Lower Cretaceous rocks of the Vértes-somló Formation (Lower Albian), Tés Formation (Middle Albian), and Pénteskút Formation (Upper Albian-Lower Cenomanian) from the Bakony, Vértes and Gerecse Mountains of Transdanubian Central Mts. It may be seen that these are largely striate, verrucate, foveolate, and foveo-reticulate in sculpture, and that they show a great resemblance to recent spores of the Schizaeales order. We distinguished the following 13 formspecies in our material on a morphological basis:

Corniculatisporites magniobatus (BOLCH. 1953) KUVAEVA 1972*Corniculatisporites virgatus* (DEÁK 1963) KUVAEVA 1972*Corniculatisporites alekhinii* (BOLCH. 1953) KUVAEVA 1972*Corniculatisporites tudariensis* KUVAEVA 1972*Corniculatisporites bolchovitinae* KUVAEVA 1972*Corniculatisporites auritus* (SINGH 1971) n. comb.*Corniculatisporites nemanicensis* (PACLTÓVÁ 1961) n. comb.*Cicatricosporites phaseolus* (DELC.&SPR. 1955) W. KR. 1959.*Verrucatosporites constrictus* (BOLCH. 1953) W. KR. 1959.*Microfoveolatosporis baconicus* n. sp.*Microfoveolatosporis surensis* n. sp.*Microfoveolatosporis csaszari* n. sp.*Microfoveolatosporis gallicus* (DEÁK&COMBAZ 1967) n. comb.

The study of the spores from Lower Cretaceous assemblages convinces us that the trilete spores of the families of the ancient Schizaeales order (Anemiaceae, Lygo-

diaceae, Mohriaceae and Klukiaceae) play a dominant part compared to the spores and pollen of the other plant groups. Thus the Schizaeales order experienced its acme-stage in the Lower Cretaceous. The monolete spores are phylogenetically younger than trilete spores, probably the monolete spore-producing genera and species developed later than the trilete spore possessing species within a given order or family.

Leaf histological and other studies, have established that among the recent genera *Schizaea* shows phylogenetically younger characteristics than the *Lygodium*, *Anemia* and *Mohria* genera. It may be supposed that the monolete spore species of the Schizaeaceae already began to differentiate in the Lower Cretaceous and that already by the Albian age palynologically valuable species and characteristics may be found.

On the basis of the above it is our opinion that most of spores dating from the Albian (here one can place several, including the smooth spores of the *Laevigatosporites*, because among the currently living species, most *Schizaea* have laevigate spores) are representatives of the Schizaeaceae family, and that the Polypodiaceae family only later developed in the branching progression.

In the Lower Cretaceous, — among the schizaeaceous monolete spores- the *Corniculatisporites* appeared first; it has the largest number of individuals and species in the Albian, and even at the Albian-Cenomanian boundary.

It is one of the „leading fossils“ in the Turrillites marl of Bakony Mts (Upper Vraconian).

Microfoveolatosporis is, however, a more frequent form of the clayey-marl deposits of Bakony and Vértes Mts (Middle Albian).

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CHANGE IN LEAF PIGMENTS DURING AUTUMN COLOURATION

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Abstract

Over three autumns (1972, 1973, 1974) we investigated the transformation of pigments in the leaves of four tree-like shrubs and one sub-shrub. The pigments were separated with thin-layer chromatography. The changes in pigments in the green, yellowish-green, and yellow leaves were measured and compared with one another.

- (1) It seems to be a general tendency that during the autumn colouration of leaves chlorophyll *a* decomposes faster than chlorophyll *b*. We attribute this phenomenon to the stronger light sensitivity of the chlorophyll-*a* molecule.
- (2) In the withering leaves of some species, the decomposition of chlorophyll *b* may also be faster or the same as that of chlorophyll *a*. Thus, during the autumn colouration of leaves, we can observe three types of chlorophyll *a/b* ratio development. We attribute this peculiarity of the „species” to the varying strength of the chlorophyll-membrane bond and to the varying presence of anthocyan.
- (3) The degradation of chlorophyll *a* is followed fastest by carotene.
- (4) In the course of the autumn decomposition lutein manifested itself as stablest of the carotenoids. The amount of epoxi-carotenoids in the withering leaves may rise or fall.

Introduction

In the course of ontogeny the amount and ratio of chlorophylls, hydrocarbon-, hydroxi- and epoxi-carotenes characteristically changes in the leaf. The autumn pigment changes most frequently indicate transformation and degradation. But new carotenoid synthesis may also occur in the ageing leaves.

Willstätter and STOLL (1918) made a scientifically historical statement concerning autumn pigment degradation. TSWETT (1911) published that in the autumn leaves carotene is almost completely transformed into xanthophylls.

KUHN and BROCKMANN (1932) established that the „autumn pigments” in nature are not carotenes but esterified xanthophylls.

According to KARRER and WALKER (1934), autumn pigments are the products of the degradation of carotenes and xanthophylls. SCHERTZ (1929) was the first to really observe a seasonal changes.

But he did not separate chlorophylls and carotenoids. WOLF (1956) studied the chlorophyll *a/b* ratio in the autumn leaves. Concerning the autumn change in the pigment content of leaves, there are but few literary data to be found. According to STRAIN's comprehensive studies (1938, 1959) on autumn leaves during autumn colouration the amount of carotenes decreases and that of xanthophylls increases.

In the pericarp of the green paprika (*capsicum*) of leaf origin, in addition to the carotenoid transformations which are similar to those in foliage-leaves, there are

also differences. CHOLNOKY (1937) and CHOLNOKY *et al* (1955) established that in the green berry-fruit of the paprika during ripening, the chlorophyll content decreases steadily, and the carotenoid (capsanthin, capsarubin, etc.) content increases. β -carotene is transformed into neoxanthin, α -carotene into lutein, and these epoxidate while ripening occurs.

With thin-layer chromatography the transformation of pigments in the leaves of four ligneous plants and one sub-shrub plant was investigated over three autumns (1972, 1973, 1974). After determining and evaluating hundreds of measured results, we looked for answers to the following problems:

1. Is the degradation of chlorophylls uniform or does the ratio of chlorophyll a/b change?
2. What is the connection between the amounts of chlorophylls and carotenoids in the course of pigment decomposition?
3. How do carotenes, hydroxi- and apoxi-carotenes develop in the autumn?

Materials and Methods

In our investigations we used the green, yellowish-green, and yellow leaves of *Cercis siliquastrum* L., the green-leaved common birch (*Betula pendula* ROTH.), *Rubus idaeus* L., *Betula pendula* var. *purpurea* (ANDRÉ) SCHNEID., and *Robinia pseudo-acacia* L. The entirely developed, normal leaves were gathered from the garden of the Ady-square building of the University, always at the same time, 8 o'clock a.m. During sampling, we took into consideration that the leaves should possibly be the same age and come from the same position on the shoots. From the leaves disks of 1 cm diameter were cut out and extracted by the method of MARÓTI—GABNAI (1971). Then the pigments were separated and measured.

Results

During the autumn leaf colouration, the pigments in the leaves of the species investigated changed in different ways. In the green, yellowish-green, and yellow leaves the chlorophyll content relating to the dry matter develops in the following way:

Table 1. Chlorophyll mg/100 g dry-matter content of leaves of different ages and colours.

Species	Pigments	green leaf		yellowish-green leaf		yellow leaf	
		mg/100 g	chl. a/b	mg/100 g	chl. a/b	mg/100 g	chl. a/b
<i>Cercis s.</i>	Chl. a.	299,3	4,34	128,2	3,90	17,6	3,45
	Chl. b.	69,0	—	32,9	—	5,1	—
<i>Betula pendula</i>	Chl. a.	348,0	4,71	87,4	4,48	3,7	0,84
	Chl. b.	73,9	—	19,5	—	4,4	—
<i>Betula p. v. purpurea</i>	Chl. a.	328,0	5,14	104,8	6,02	20,6	5,72
	Chl. b.	63,8	—	17,4	—	3,6	—
<i>Robinia p.</i>	Chl. a.	499,7	4,46	144,7	3,95	81,6	4,10
	Chl. b.	112,1	—	36,6	—	19,9	—
<i>Rubus idaeus</i>	Chl. a.	352,9	4,45	145,7	4,73	23,6	4,00
	Chl. b.	79,3	—	30,8	—	5,9	—

During the degradation of leaves, the chlorophylls in all samples decompose considerably. In the species investigated, the degradation of chlorophyll *a* and chlorophyll *b* is of different degree. On the basis of the change in the *a/b* ratio of chlorophylls, three types could be separated:

a) Chlorophyll *a* decomposes faster than chlorophyll *b*, therefore the *a/b* ratio decreases. This may be observed in the leaves of *Cercis* s. and *Betula pendula*. (Fig. 1).

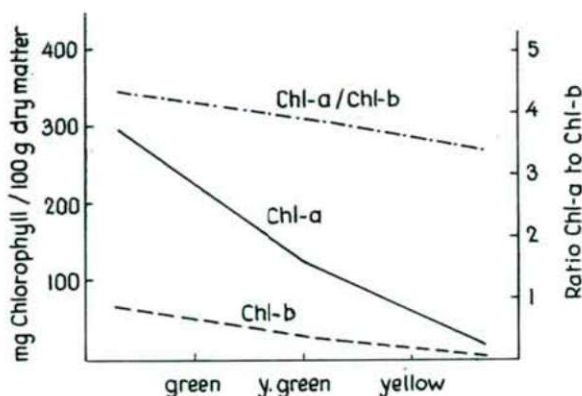


Fig. 1. Change in the chlorophyll content and the *a/b* ratio in the different leaves of *Cercis* s.

b) Initially, in the withering leaves, the decomposition of chlorophyll *b* is faster, therefore the chlorophyll *a/b* ratio at first increases and then decreases. (Fig. 2).

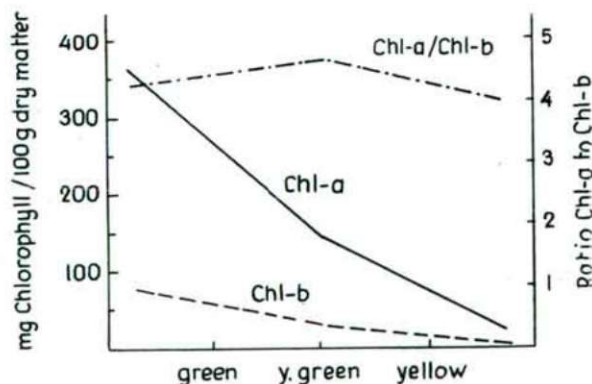


Fig. 2. Change in the chlorophyll content and the *a/b* ratio in the leaves of different colours of *Robus idaeus*.

c) Initially, the decomposition of chlorophyll *a* is faster, then it becomes slower in a later phase of withering. Consequently, at first the chlorophyll *a/b* ratio decreases, then somewhat increases. (Fig. 3).

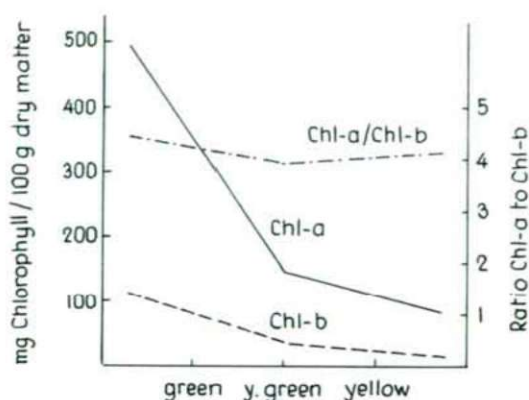


Fig. 3. Change in the chlorophyll content and the a/b ratio in the leaves of different colours of *Robinia pseudoacacia*.

In the course of the autumn colouration of leaves, apart from chlorophylls, the change in carotenoids was also measured. We studied mainly the development of the ratio of carotenes, hydro- and epoxi-carotenoids.

1. Most carotenes and hydroxi-carotenes (lutein+zeaxanthin) are contained in the photosynthetically active green leaves. These pigments do not accumulate in the course of withering but decompose. The amount of carotene decreases in approximately direct ratio to the decomposition of chlorophyll b (Table 2).

Table 2. Change in the amount of carotenes during autumn colouration of leaves. The values are relative to mg carotene/100 g dry matter. The carotene content of the green leaf was taken as 100 per cent.

Species-investigated	green leaf	yellowish-green leaf		yellow leaf	
	mg/100 g	mg/100 g	per cent	mg/100 g	per cent
<i>Cercis s.</i>	32,7	12,8	39,1	3,4	10,4
<i>Betula p.</i>	30,2	12,1	40,1	10,3	34,1
<i>Rubus i.</i>	34,8	13,2	37,9	8,1	23,3
<i>Betula p. v. purpurea</i>	41,7	20,1	48,2	12,8	30,6
<i>Robonia p.</i>	66,8	35,5	53,1	27,4	41,0

2. During autumn colouration, the amount of hydroxi-carotenes diminishes less than the carotene content. The degradation of lutein in the leaf of *Betula p. var. purpurea* is remarkably small (Tab. 2).

Table 3. Change of the lutein + zeaxanthin content in the leaves of different colours. The values refer to mg pigment/100 g dry matter. The hydroxi-carotene content of the green leaf was taken as 100 per cent.

Species investigated	green leaf	yellowish-green leaf		yellow leaf	
	mg/100 g	mg/100 g	per cent	mg/100 g	per cent
<i>Cercis s.</i>	52,3	40,5	77,4	17,2	32,9
<i>Betula p.</i>	79,0	56,5	71,5	35,2	44,6
<i>Rubus i.</i>	51,0	29,7	58,2	23,6	46,3
<i>Betula p. var. pur.</i>	69,5	51,5	74,1	49,3	70,9
<i>Robinia p.</i>	108,2	64,8	59,9	58,5	54,1

3. The change in the epoxi-carotenes (antheraxanthin, violaxanthin, neoxanthin, during autumn colouration of leaves, takes place in a way characteristic of the single species (Table 4).

a) Most violaxanthin and neoxanthin are contained in the green leaf, and these pigments also decompose gradually. This may be observed in the leaves of *Cercis s.*, *Rubus i.*, *Betula p.*, and *Robinia p.* (Table 4).

Table 4. Change in the amount of epoxi-carotenes during the autumn colouration of leaves. The values refer to mg epoxi-carotene/100 g dry matter. The antheraxanthin, violaxanthin, and neoxanthin content of the green leaf was taken as 100 per cent.

Pigments		green leaf	yellowish-green leaf		yellow leaf	
		mg/100 g	mg/100 g	per cent	mg/100 g	per cent
<i>Cercis s.</i>	antherax.	6,5	5,1	78,5	2,4	36,9
	violax.	23,4	11,5	49,1	1,9	8,1
	neox.	18,8	11,0	58,5	3,4	18,1
<i>Betula p.</i>	antherax.	7,2	9,3	129,1	11,9	165,3
	violax.	21,0	10,3	49,0	13,7	65,2
	neox.	18,1	11,6	64,1	8,0	44,2
<i>Rubus i.</i>	antherax.	7,8	4,9	62,8	4,7	60,3
	violax.	33,4	12,4	37,1	5,2	15,6
	neox.	17,3	8,9	51,4	5,3	30,6
<i>Betula p. var. purpurea</i>	antherax.	3,4	6,9	202,9	11,8	347,0
	violax.	23,0	29,7	129,1	21,3	92,6
	neox.	10,5	12,6	120,0	8,8	83,8
<i>Robinia p.</i>	antherax.	9,7	10,5	108,2	14,8	152,6
	violax.	35,5	27,2	76,6	19,4	54,6
	neox.	24,5	24,3	99,2	17,9	73,1

- b) Antheraxanthin accumulates in the yellowish-green and yellow leaves of the *Betula p. var. purpurea*, *Betula p.*, and *Robinia p.* species.
- c) The total epoxi-carotene accumulates in the yellowish-green leaves of *Betula p. var. purpurea*.

Discussion of results

Willstätter and STOLL (1918) found that in the leaves should precede „in the autumn“ the ratio of chlorophyll *a/b* does not change. Several authors, however, namely: RUDOLF (1934), NAGEL (1940), SEYBOLD (1943), EGLE (1944) Jeffrey and GRIFFITH (1947), STRAIN (1949), WOLF (1956), GOODWIN (1958), established that chlorophyll *a* decomposes faster than chlorophyll *b*, in green leaves as a result of various conditions. SANGER (1971) demonstrated that in the leaves of *Corylus americana*, *Populus tremuloides*, and *Quercus ellipsoidalis* the chlorophyll *a/b* ratio falls in autumn.

The different rates of chlorophyll destruction are explained by EGLE (1944) and GOODWIN (1958) by the different sensitivities to acid. According to them chlorophyll *a* decomposes faster because it is less resistant to the acid environment than chlorophyll *b* is.

Our results partly differ from the findings of the above authors. Chlorophyll *b* can also decompose faster than chlorophyll *a* does. Therefore, the chlorophyll *a/b* ratio may rise, too during the autumn colouration of leaves. (Cf. in Table: *Betula p. var. purpurea* and *Rubus i.*).

Apart from a few exceptions, it seems to be common however that in autumn chlorophyll *a* decomposes faster than chlorophyll *b* does. We cannot accept completely the different sensitivity to acid for an explanation of the different decomposition.

The chlorophyll *a* molecule in solution (ether, alcohol, acetone) decomposes faster under the influence of light than does chlorophyll *b* (MARÓTI, 1970). The autumn colouration of leaves is connected with the destruction of the thylacoid membrane. It follows from the different light sensitivity of the chlorophylls released that in the majority of plants chlorophyll *a* decomposes faster.

In the leaves of *Rubus i.* and *Betula p. var. purpurea* in some red pigments, anthocyanins, accumulate during the autumn colouration of leaves. The leaves, therefore, do not become yellow, but red. It is to be supposed that one of the tasks of the anthocyanins is to protect chlorophyll *a* from the light-induced destruction.

In case of *Robinia p.* we consider it possible that part of the chlorophyll *a* is more strongly connected to the thylacoid membrane, slowing its rate of decomposition a while.

We investigated the pigment content of coloured leaves for three autumns (1972, 1973, 1974). We observed two types of chlorophyll decomposition: pheophytinic decomposition, and the decolorization of chlorophylls.

a) Pheophytinic decomposition of chlorophylls

If the temperature reaches even a value of -2°C in the small hours of the morning, then ice-crystals form in the cells. These destroy the membranes, and permit the cellfluid of low pH to get into the plastids. The fall-out of Mg from the chlorophyll, and thus the formation of pheophytin, is promoted by the H^{+} -ions. On the other hand, it is known on the basis of the investigations of KRINSKY (1966), SAPOZHNIKOV (1969), MARÓTI and SZAJKÓ (1972) that in the dark (at night) mainly epoxidative reactions take place. These already become slower at 15°C , and at about 0°C they are completely hindered. As the carotenoids are not epoxidized in the cold, they cannot protect the chlorophylls against photodestruction.

b) Autumn decolourization of chlorophylls

In case of a long, mild autumn (with 15°C to -1°C temperature in the small hours of the morning (the electrontransport chain between the two photochemical systems (supposedly at the cytochromes) may be blocked. The photolysis of water goes on, the conjugated double-bonds of the chlorophylls are saturated by the „H-atoms“ produced, and the oxygen favours the accumulation of epoxi-carotenes.

Peculiarities of the decomposition of carotenoids

In the autumn leaves the decomposition of chlorophylls may occur some days earlier, and to a more considerable degree, than that of the carotenoids. In case of the five studied species, carotene is the most sensitive and follows the decomposition of chlorophyll the fastest. According to STRAIN (1959), during the autumn colouration in the leaves, the amount of carotenes falls. As a result of oxidation these are transformed into hydroxi- and epoxi-carotenoids. The high level of lutein in the greenish-yellow leaves could be explained by the facts discussed above.

According to SANGER (1971), neoxanthin and violaxanthin are the most sensitive and in Autumn they decompose the fastest. Our results, however, do not support this conclusion. In the leaves of *BETULA P. var. PURPUREA* and *ROBINIA P.* only epoxi-carotenes accumulate. Supposedly the epoxidation of hydroxicarotenes causes the rise of, or the lesser fall in, antheraxanthin, neoxanthin, and violaxanthin.

In the transformation of carotenoids the peculiarities of species and climatic factors are mostly unknown. This may be the cause of the difference between the literary data.

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CHANGE IN THE ENDOGENOUS GIBBERELLIN CONTENT DURING SWELLING OF LUPINUS ALBUS L. SEEDS

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Abstract

The quantitative change in the various gibberellin forms occurring in *Lupinus albus* L. seeds was investigated during swelling with the lettuce hypocotyl and barley endospermium tests.

We demonstrated various gibberellin forms from dry seeds, including the free gibberellin-like substances. Our results show that probably not the appearance but the suitable level of the free gibberellins is necessary to germination. The level of the free gibberellin-like substances increased by leaps and bounds as early as in the first few hours of swelling, achieving its maximum in the barley endospermium test in the sixth, and in the lettuce hypocotyl test in the eighteenth, hour of swelling. Considerable biological activity was observed in the butanol-soluble fraction, probably due to the action of nonspecific glucosidases. The amount of the gibberellin-like substances in the butanol-soluble fraction already showed a declining tendency in the early period of swelling. A change of similar character was observed in the case of the TCA-insoluble fraction, as well.

Between the endogenous gibberellin contents of the seeds swelled in the light and in darkness no difference was observed.

The quantitative increase in the free gibberellin-like substances is supposedly the result of the release of bound forms because the emergence of the radicle is not inhibited by CCC, the inhibitor substance of the biosynthesis of gibberellin.

Introduction

During maturing of the seeds, the transformation of free gibberellins into bound gibberellins can be observed (SEMBDNER et al., 1968). The results connected with the role played by bound gibberellins in the germination of seeds are not unambiguous. There are but few investigations of this character in the literature to be found, and these data are concerned with the conditions after the emergence of the radicle.

According to the statement of BARENDSE et al. (1968), the pea seedling is not sensitive to AMO—1618. For this reason they suppose that the increase in gibberellin content is not connected with synthesis. At the same time, seedling *Pharbitis* can be inhibited by AMO—1618 immediately after germinating; therefore, according to BARENDSE et al. (1968) it is not proved that the bound gibberellins play a role in the early development of *Pharbitis*. In the opinion of SEMBDNER et al. (1968), in the germination of beans gibberellin is de novo synthesized.

The change in the endogenous gibberellin content before the emergence of radicle was investigated in some cases in seeds in a state of deep rest (ROSS and BRADBEER, 1971; SZALAI and NAGY, 1974) but these statements only refer to a change in the free endogenous gibberellin content, without comprising the role of bound gibberellins.

If we take germination in a stricter sense of the word, meaning by that the activation of the cells of the seed, and regarding the observable germination, i. e., the protrusion of some part of the embryo from the seed as a result of growth (MAYER and POLJAKOFF—MAYBER, 1963), then we have to perform the investigation of the quantitative change in the endogenous gibberellin content, taking place in the germinating seeds, in the period preceding the emergence of radicle. This period is generally called swelling. But the physical processes of swelling and the physiological processes of germination cannot be isolated from each other with a sharp borderline.

The investigation of the change in the endogenous gibberellin forms, as well as of the problem of how the change of the endogenous free gibberellin level takes place before the radicle starts was carried out by using an object of a well-known high endogenous gibberellin content.

Materials and Methods

For our investigations we used *Lupinus albus* L. seeds obtained from the Gyulatanya-Station of the Agricultural Research Institute of Nyir (a district in North-Eastern Hungary).

Measurement of the change in weight of seeds during swelling

50—50 seeds were swelled, at 20 °C, with plenty of water. The seeds, removed from the water and dried and blotted with filter-paper, were weighed on an analytic balance in every four hours. The dry-matter content of seeds was determined in a desiccator at 105 °C, after being dried till achieving weight equilibrium.

Extraction and chromatographing of gibberellins

50 seeds were extracted after grinding with 80 per cent cold methanol of tenfold quantity in a refrigerator for 2×24 hours. The united methanolic extract was isolated according to the method of HARADA and YOKOTA (1970), into ethylacetate-soluble and butanol-soluble acid fractions. The ethylacetate-soluble acid fraction was distilled at reduced pressure and chromatographed on a silica gel G layer. For the development, a diisopropylether: acetic acid (95:5) solvent was used (REINHARD et al., 1964).

The butanol-soluble acid fraction was divided into two parts. One of these was chromatographed after being distilled at reduced pressure. The solvent was chloroform: methanol: acetic acid: water (40:15:3:2) (HARADA and YOKOTA, 1970). The other part was hydrolysed with 1 N H₂SO₄, at 100 °C, for two hours (YOKOTA et al., 1969).

The gibberellins released during hydrolysis were extracted with ethylacetate, then the ethylacetate extract was distilled at reduced pressure and chromatographed with thin layer. The tissue-homogenizate, a residue after the methanolic extraction, was suspended in phosphate-buffer (pH 8.0) after distilling the remains of the solvent, and centrifuged after standing for 24 hours. After being centrifuged, the supernatant was treated with 10 per cent trichloroacetic acid (TCA). After being centrifuged again, the precipitate was hydrolyzed with 2 N NaOH, at 40 °C, for four hours. After being acidified with hydrochloric acid (pH 2.8), the gibberellins released were extracted with ethylacetate, distilled, and chromatographed with thin layer.

Lettuce hypocotyl test

After distilling the residue of the solvent, the chromatogram developed was divided into ten equal parts and the silica gel was scraped down into Petri dishes of 7 cm Ø. The powder was covered with a filter-paper disk and wetted with 3 ml distilled water. The biological activity was measured by the method of Frankland and WAREING (1960). A layer, developed and tested, and containing no plant-extract, was used as control. For the investigations, the lettuce variety "King of May" was used.

Barley endospermium test

The silica gel scraped down from the chromatogram strips was eluted with ethylacetate, or n-butanol. Then after being centrifuged, it was distilled dry at reduced pressure, dissolved in acetate-buffer (pH 4.8) containing 2 ml 20 µ M CaCl₂, filtered through a bacterial filter, poured into a 5 cm Ø Petri dish, and tested with barley endospermium under sterile conditions, according to the method

of JONES and VARNER (1967). After being incubated for 24 hours, to 1 ml of the incubation solution 1 ml of 1 per cent starch-solution prepared with acetate-buffer (pH 4.8) containing 1 ml 20 μ M CaCl_2 was added. The incubation was carried out at 40 °C, for ten minutes. Then 1 ml was removed and we added to it 10 ml solution of 0.0003 N $\text{KJ}-\text{J}_2$, prepared with hydrochloric acid. The optical density of the solution was measured at 580 nm.

The amount of α -amylase was calculated by means of the formula given by JONES and VARNER (1967). As a control, a developed and tested layer was used, containing no plant extract.

Treatment of the seeds with a chlorocholine-chloride (CCC) solution

Seeds 50 per Petri dish were germinated in Petri dishes containing filter-paper with 500, and 1000 ppm CCC, respectively, in a 25 °C thermostat. Control seeds were placed a Petri dish containing some filter-paper wetted with distilled water.

Results and discussion

1. Change in weight of the seeds during swelling

The change in weight of the *Lupinus albus* seeds is illustrated in Fig. 1. As seen in the figure, the seeds swelled rapidly. They take up 69 per cent of the total water quantity taken during the whole length of swelling time by the fourth hour, and 78 per cent by the seventh hour.

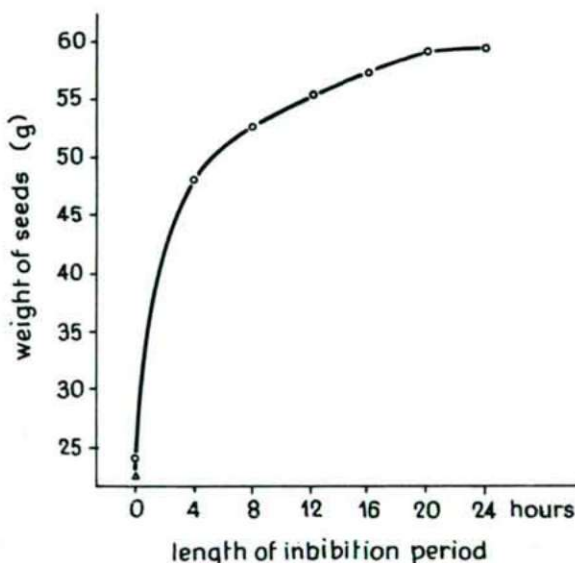


Fig. 1. Change in weight of 50 *Lupinus albus* seeds during swelling, at 20° C.

During the length of swelling time we did not observe any essential change in the dry-matter content of the seeds.

2. Quantitative change in the endogenous free gibberellin—like substances during the swelling of seeds

The change in the endogenous gibberellin content during the swelling of *Lupinus albus* seeds was measured with two kinds of biological tests, because the biological activity of the various gibberellins was different in the different tests (REEVE, 1974). The barley endospermium test is sensitive to lower gibberellin concentrations than

the lettuce hypocotyl test; it is not impeded by the possible solvent residue in the extract. The lettuce hypocotyl test, on the other hand, is sensitive to a wider spectrum of gibberellins (JONES and VARNER, 1967).

The quantitative change of the endogenous free gibberellin-like substances during swelling is shown in Fig. 2 (under A and B).

With the barley endospermium test, the presence of three gibberellin-like substances of different Rf-values was demonstrated, showing maximum activity in the sixth hour of swelling. The presence of these substances was also indicated by the lettuce hypocotyl test (Fig. 2, B), as well as an active spot of the position Rf 0,3—0,4. To the gibberellin-like substance in the position Rf 0,3—0,4 the barley endospermium

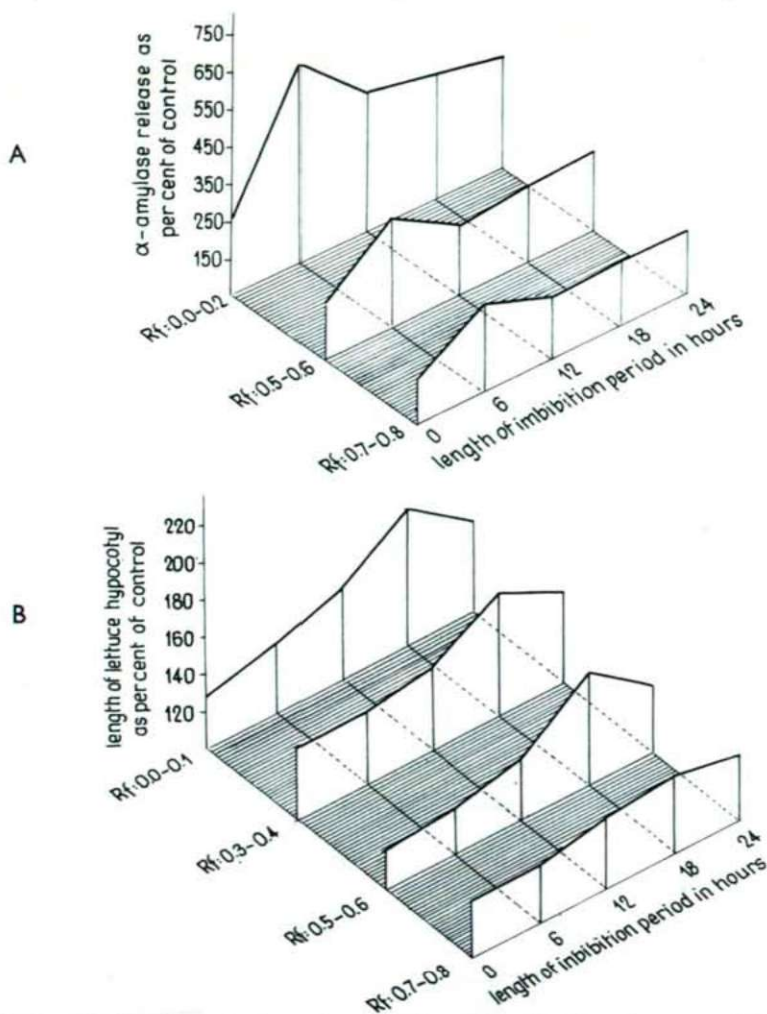


Fig. 2. Quantitative change in the endogenous free gibberellin-like substances of the *Lupinus albus* seeds, during swelling, measured as compared to 100 seeds, with the barley endospermium test (A) and the lettuce hypocotyl test (B).

test was not sensitive. We observed the maximum biological activity in the lettuce hypocotyl test in the 18th hour of swelling. The cause of the time difference between the maxima of the two tests may have been in connection with the different gibberellin-sensitivity of the tests. (In the case of the barley endospermium test the maximum enzyme activity was obtained at 0,1 ppm; in the case of the lettuce hypocotyl the maximum growing with extension was attained at a concentration of 10 ppm GA_3).

3. Quantitative change in the gibberellin-like substances in the butanol-soluble fraction during the swelling of seeds

According to our results, the butanol-soluble fraction show significant biological activity in both tests.

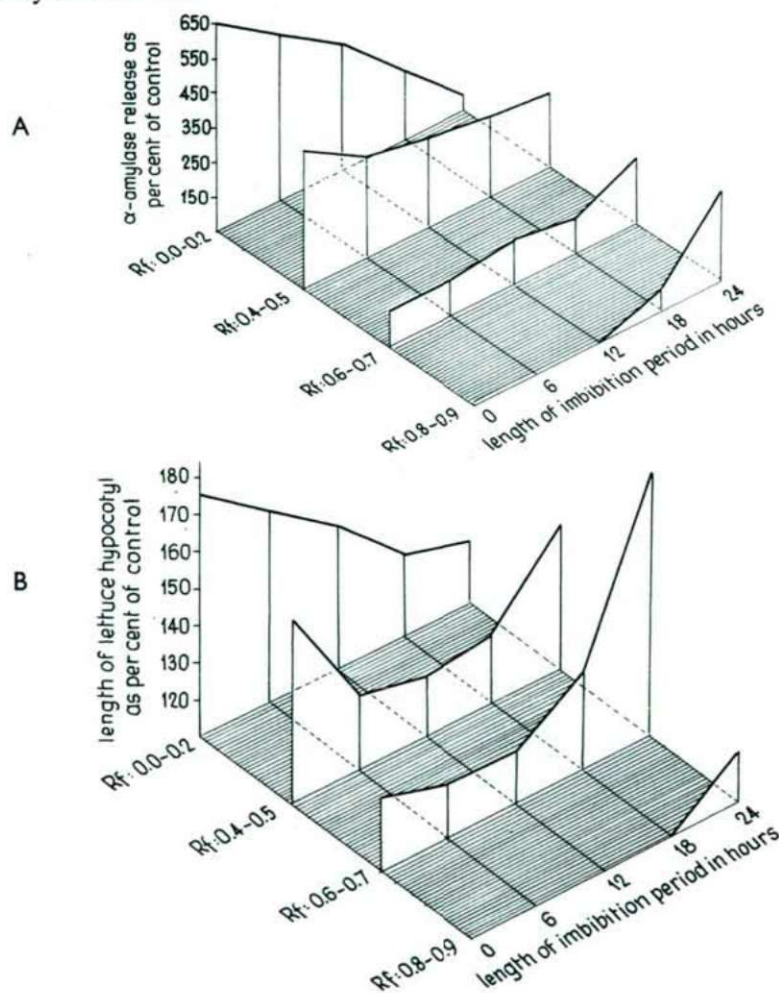


Fig. 3. Quantitative change in the gibberellin-like substances in the butanol-soluble fraction, during the swelling of *Lupinus albus* seeds, measured as compared to 100 seeds, with the barley endospermium test (A) and the lettuce hypocotyl test (B).

The biological activity observed may have been a result of the effect of gibberellins released by the non-specific glycosidases. Under normal conditions, these glycosidases do not encounter the endogenous gibberellin conjugata (Reeve, 1974).

The quantitative change in the gibberellin-like substances in the butanol-soluble fraction is illustrated in Fig. 3 (under A and B).

The quantity of the gibberellin-like substance of position Rf 0,0—0,2 tends to decline, according to the results of both barley endospermium and the lettuce hypocotyl test.

After an initial decrease the quantity of the gibberellin-like substance of positions Rf 0,4—0,5 and Rf 0,6—0,7 increased 24 hours after the beginning significantly.

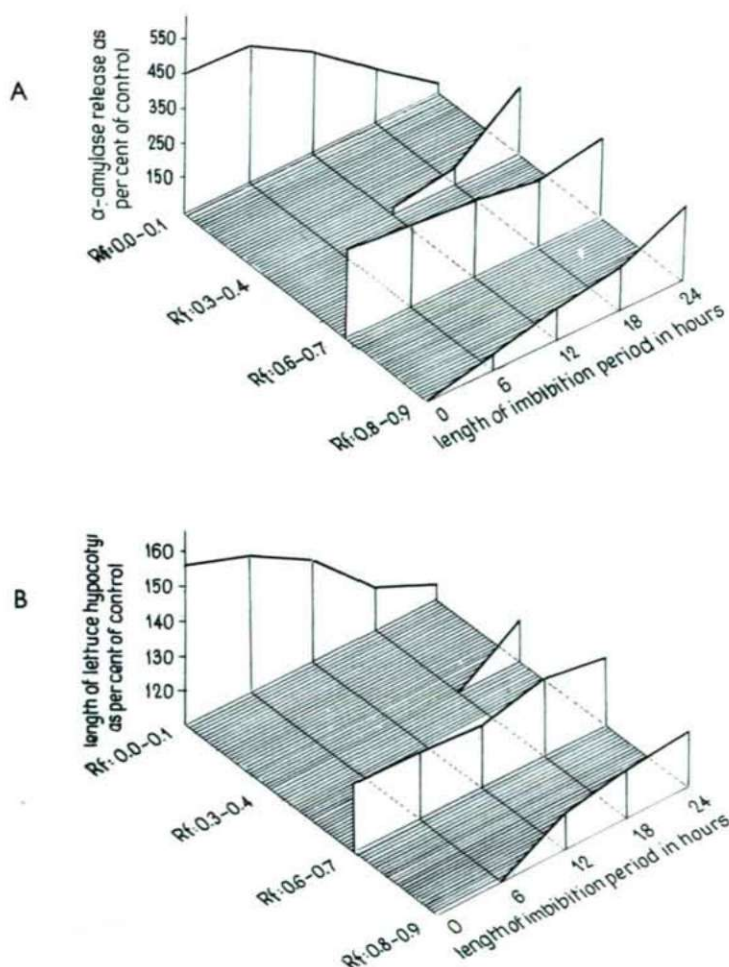


Fig. 4. Biological activity of the butanol-soluble fraction, after acid hydrolysis, measured as compared to 100 seeds, with the barley endospermium test (A) and the lettuce hypocotyl test (B).

The gibberellin-like substance in position Rf 0,8—0,9 could only be demonstrated from the 12th, and 18th hour of swelling respectively.

The tendency of the quantitative change in the gibberellin-like substances in the butanol-soluble fraction is not identical. The differences observed are difficult to interpret as we do not know if any of the gibberellin-like substances occurring in the seed act as regulators of germination.

The results of the biological testing after acid hydrolysis of the butanol-soluble fraction are shown in Fig. 4 (under A and B).

A quantitative change of similar tendency was seen in the results of testing before hydrolysis, but the biological activity was in any case lower. In the case of hydrolysing with β -glycosidase the results achieved were similar, as well.

The Rf-values of the biologically active substances obtained after the acid hydrolysis of the butanol-soluble fraction and of the free gibberellin-like substances in the ethylacetatic fraction do not always agree with one another. This, and the fact that with the α amylase test, after the hydrolysis of the butanol-soluble fraction, more gibberellin-like substance could be demonstrated than in the ethylacetatic fraction show that in the course of swelling we probably also have to reckon with interconversion. A convincing answer to this question can be given after the investigation of the qualitative change in the endogenous gibberellins.

4. The quantitative change in the gibberellin-like substances of the TCA-insoluble fraction during swelling

The presence of protein-bound gibberellins was established by a number of authors (McCOMB, 1961; JONES, 1964; HAYASHI and RAPPAPORT, 1962; REINHARD and SACHER, 1967). The nature of the gibberellin-protein complexes is not known, but the fact that gibberellin-like substances can be easily isolated from protein, shows that they are linked together with comparatively weak bonds.

These complexes precipitate as a result of the organic solvent applied during extraction. The amount of the gibberellins bound to the macromolecules can therefore be determined by using the tissue-remains after the evaporation of the solvent residues (JONES, 1964).

The biological activity, observed after the alkaline hydrolysis of the TCA-insoluble fraction and its extraction with ethylacetate at acid pH, is shown in Fig. 5 (under A and B).

In the TCA-insoluble fraction, a small amount of gibberellin-like substance was demonstrated with both tests. The tendency of the quantitative changes is similar to that of the gibberellin-like substances in the butanol-soluble fraction.

5. The effect of CCC-treatment on the germination of seeds

In order to decide if the increase in the endogenous free gibberellin content observed during the swelling of *Lupinus albus* seeds results from the release of bound forms, or from de novo synthesis, we germinated seeds in CCC solutions of 500, and 1000 ppm concentration. CCC is a biosynthesis retardant often applied to both lower and higher plants (HARADA and LANG, 1965; JONES and PHILLIPS, 1966). It impedes the cyclization process of geranyl-geranyl-pyrophosphate. Our results are illustrated in Fig. 6. According to our investigations, the emergence of the radicle is not impeded.

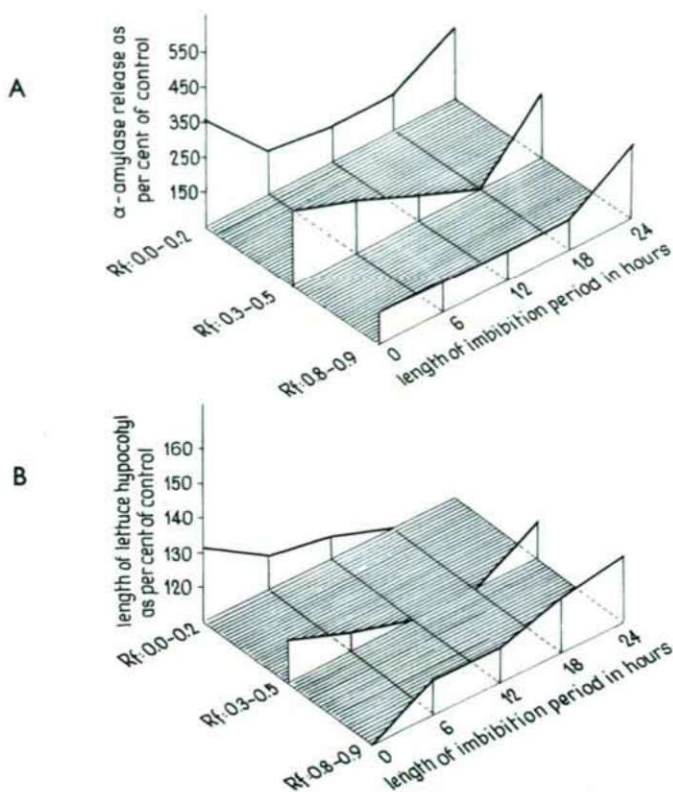


Fig. 5. Quantitative change in the gibberellin-like substances of the TCA-insoluble fraction, during the swelling of *Lupinus albus* seeds, measured as compared to 100 seeds, with the barley endospermium test (A) and the lettuce hypocotyl test (B).

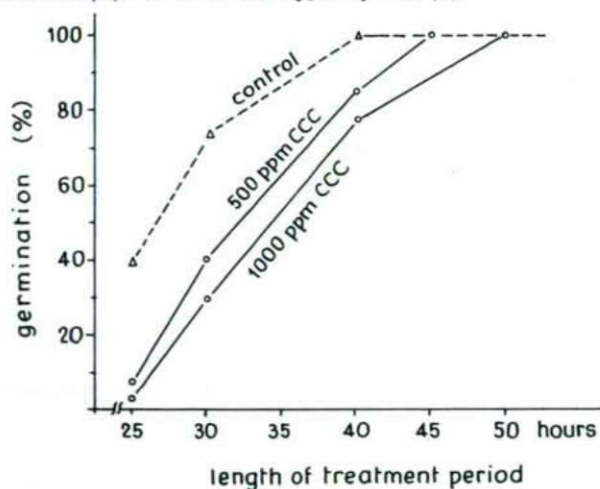


Fig. 6. Effect of CCC treatment on the germination of *Lupinus albus* seeds.

This means that the increase in the endogenous free gibberellin content is probably due to being released, and that is the main moment during swelling. As germination is retarded by the CCC-treatment as compared to the control, we possibly have to also reckon with minor de novo synthesis, and the speed of germination depends upon that.

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EFFECTS OF BIOLOGICALLY-ACTIVE SUBSTANCES ON THE AMINO ACID METABOLISM OF ISOLATED LUCERNE SHOOTS IN THE CASE OF LIVE-WILTING

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Abstract

The essential amino acids, proline and amides accumulate to an extremely great extent in excised lucerne shoots if these are left spread out in light to lose their water progressively over two days while still alive (we have termed the phenomenon "live-wilting").

The total free amino acid content of control shoots which are dried immediately after cutting-off is very low (1.83% of the dry matter). As a consequence of live-wilting for 2 days, this content is 8.15%, i.e. an increase of 4.45 times. Our results indicate that the digestibility quotient, the biological value and the protein-utilization of green-fodder plants can be increased by around 100% with the artificial live-wilting method (by increase of the free protein-forming amino acids).

It was found that if the shoots are treated with biologically-active substances after the cutting-off, during the live-wilting in the following 2 days the total free amino acid content can be further increased considerably. Treatment with indole acetic acid (20 mg/l) and joint treatment with indoleacetic acid (20 mg/l)+abscisic acid (5 mg/l) led to total free amino acid increases of 20% and 60%, respectively, compared to a control treated only with water.

Although treatment with abscisic acid alone did not increase the total amino acid values of the isolated shoots, it did decrease the water turnover of the shoots by 30%, by closing the stomata. This water turnover decrease was not antagonized either by the joint effect of indoleacetic acid + gibberellic acid + furfurylaminopurine employed with the abscisic acid.

It was found that, when carefully dried at 70 °C and granulated, the young lucerne shoots containing an elevated amino acid content as a result of live-wilting can also be utilized as a food for humans, if sufficiently spiced. This preserved food would form a sure protein basis for feeding purposes in protein-poor countries.

At present the live-wilting procedure on isolated shoots is the most easily performable and therefore the cheapest method of producing by biological means natural amino acid mixtures representing high-level protein-utilization.

Introduction

At the time of a severe water-deficiency in the case of field-grown herbaceous plants, the intensity of photosynthesis decreases, the starch, protein and nucleic acid contents do not increase, and the growth ceases. At the same time, the synthesis and accumulation of the free amino acids are enhanced (KUDREV and TYANKOVA, 1966; SANTARIUS and ERNST, 1967; PÁLFI, 1968ab, 1971; LEWITT, 1972; PERDRIZET, 1974; VALLEE, 1973; WALDREN and TEARE, 1974). As a result of the water-deficit, in the leaves there is an accumulation primarily of the essential amino acids, the amides, and particularly proline.

If the shoots are cut off and left spread out in the light to lose their water gradually during the processes of photosynthesis while the shoots are still alive, their

total amino acid content increases to a much greater extent compared with that of the intact, field-growing water-deficient plants. During this phenomenon of „live-wilting“ (PÁLFI, 1969, 1971) the isolated shoots lose 70—80% of their original water content. Such a high water-deficit can be attained mainly only in culture-vessel experiments and in the isolated shoots.

The practical importance of the water and nutrient metabolism of isolated shoots is that all cut and harvested green-fodder plants of greenstuffs undergo live-wilting for a time prior to the processing or preservation, and during this time their free, protein-forming amino acid content may increase to a considerable extent, or it may decrease, depending on the changes in the environmental factors.

By means of artificial live-wilting in a conditioned medium for 2 days, it proved possible systematically to increase the protein-forming total amino acid content of the cut-off shoots of lucerne and other fodder plants from 2.0% to 6.0—10.0%, without an accompanying decrease in the protein content (PÁLFI, 1971; PÁLFI et al., 1974ab, 1975ab). It has already been proved in animal and human experiments (RIGÓ, 1976) that a natural mixture of the protein-forming free amino-acids may be equivalent to three times the amount of proteins as regards nutrition, because of the low efficiency of digestion of the proteins.

In our experiments with isolated shoots and leaves, in only 17 of 50 herbaceous plant species belonging to 14 families did it not prove possible to detect systematically a high proline content (i. e. above 1.0% of the dry matter) on the application of live-wilting. However, in the species of „non-proline type“ too the total amino acid content increased to a high level. The majority of soft-stemmed plants are therefore of „proline-accumulating type“ (PÁLFI et al., 1973, 1974ab). It has been shown that the level of proline accumulation is primarily a species characteristic, and is connected only secondarily with the magnitude of the water-deficiency and with the degree of drought-resistance among the cultivated varieties (PÁLFI et al., 1975a).

Physiological aridity and the accompanying high total amino acid and proline contents may be induced in the leaves by the low temperature of the culture medium, by frost, or by the elevated osmotic pressure of the medium (GOAS, 1966; HUBAC, 1967; PÁLFI, 1969, 1971; BOKAREV and IVANOVA, 1971; BATES et al., 1973; HUBER, 1974; STEWART and LEE, 1974). However, we shall not deal with this phenomenon now.

It has already been established that, during the first 6—8 hours of live-wilting, changes take place in the endogenous biologically-active substances of the shoots: the concentrations of indoleacetic acid oxidase and abscisic acid (ABA) increase rapidly, while at the same time the amount of indoleacetic acid (IAA) decreases strongly (DARBYSHIRE, 1971; ITAI and VAADIA, 1971). It follows from this that the effects of such biologically-active substances as exogenous IAA and ABA may be manifested via the magnitudes of the intensities of amino acid and protein syntheses, and also by the accumulation of these substances.

A study was earlier made (PÁLFI et al., 1975ab) of the individual effects of IAA, gibberellic acid (GA_3), furfurylaminopurine (FAP), ABA and potassium ions on the water equilibrium of isolated lucerne and lentil shoots and on the free amino acid content of the shoots during live-wilting. It was found that the considerable accumulation of the protein-forming amino acids in the cut-off fodder plants during live-wilting can be further increased substantially with certain biologically-active substances.

In the first part (A) of our present experiment, a study is made of how IAA and ABA solutions absorbed into lucerne shoots at the lower part of the stem, immediately after cutting-off, affect the water turnover and the amino acid and protein metabolisms of the live-wilting shoots. In addition, the combined effect of exogenous IAA + GA₃ + FAP is examined, together with the question of whether the amino acid content in this variant changes if the treatment is combined with ABA.

Since it was earlier found (PÁLFI et al., 1975ab) that the level of amino acid accumulation is raised significantly by IAA solution during live-wilting, while exogenous ABA acts in decreasing the water turnover, in the second part (B) of our present experiments a study is made of the combined activities of these two growth substances, which have fairly opposite effects, and IAA and ABA treatments are also made individually.

Materials and Methods

Lucerne shoots grown in the field with the optimum water supply were divided into 100 g groups immediately after cutting-off (every variant was carried out in triplicate). In the course of this weighing procedure, the lower, aged leaves of the 25–30 cm long shoots were removed, or the lower part of the shoots was cut off. Every 100 g group consisted of 30 shoots. Next, 150 ml solutions of the active ingredients or the control water were poured into deep glass vessels, and the basal parts of the well-washed shoot groups were immersed for 24 hours in these solutions under illumination (Fig. 1). The shoots in one group (in triplicate) were cut up finely, immediately fixed and dried at 70 °C (fresh, control).

After the 24-hour illuminated absorption, the groups were reweighed in the water-saturated state. The shoot groups were then spread out, no longer in solution but on separate dishes, reilluminated, and a severe water-deficiency (water-losing live-wilting) was provoked to the accompaniment of a low atmospheric humidity, so that the shoot groups lost 70–80% of their water content during the 48-hour incubation. The shoots were next weighed once again (wilting weight). Finally, the shoot groups were chopped up, dried to weight constancy at 70 °C, their dry matter contents were weighed, and the material was then ground for purposes of extraction.

The paper and thin-layer chromatographic methods of amino acid analysis, the development being slowed by cooling, were reported previously (PÁLFI et al., 1972, 1973, 1974ab).

The proline was measured separately. Six different amounts of proline standards were also applied to the 18–22 band paper, with variants in triplicate (Fig. 2). After development and elution, the extinctions of the isatin blue solutions were measured spectrophotometrically.

The total amino acid, with the exceptions of proline and asparagine, was measured with the aid of the universal standard, an elution-colorimetric method being used (PÁLFI et al., 1973, 1974ab). Certain analytical details were checked on an automatic amino acid analyzer (Biocal BC 200).

The soluble total protein was measured with the method of LOWRY et al. (1951). Samples with different water contents were calculated on the basis of an identical dry matter content.

Amino acid and protein analyses were carried out on 3–5 samples and the averages are reported. If the mean error of the average result for any variant was larger than ± 5 –7%, the entire analysis was repeated.

Experimental results

(A) First part of the experiments involving absorption of the active substances and live-wilting

In the course of the absorption treatment of the isolated shoots, an interesting change in external disposition occurred in certain variants; this is illustrated in Fig. 1.

From Fig. 1 it may be stated that exogenous IAA and combinations of IAA with other active substances gave rise to almost the same degree of curvature. This curva-



Fig. 1. Absorption treatment of isolated lucerne shoots with water and with solutions of biologically-active substances. The basal parts of groups of shoots weighing 100 g were immersed in the solutions. Absorption took place from 150 ml of solution, for 24 hours. The solutions were changed every 8 hours, and their volume changes too were measured. Absorption was carried out in air at 20° C, with a humidity of 60% and under an illumination of 3000 lux. Treatments: 1=water; 2=ABA (5 mg/l); 3=IAA (20 mg/l); 4=IAA + GA₃ + FAP (20 + 50 + 20 mg/l); 5=IAA + GA₃ + FAP + ABA (20 + 50 + 20 + 5 mg/l).

ture of the shoots is not a consequence of the water-deficiency (turgor decrease), for the experimental data revealed that the absorption treatment caused maximum turgor (Table 1). From these IAA-specific epinastic curvatures of the shoots it may be concluded that the IAA solution joined into the metabolism via the absorption circulation, since its effect could be exerted only in this way. It may also be stated that neither the GA₃ administered together with the IAA, nor the FAP and the ABA, antagonized these curvatures at all. In the leaves of the shoots treated with the ABA solution, the state of the stomata was checked by microscopic study at 2-hourly intervals. Even after 6 hours' absorption, the ABA had caused all of the stomata of the leaves to close completely. This fact proves beyond any doubt the absorption, distribution and efficiency of ABA.

The amino acid analyses revealed that the total amino acid content of the shoots fixed and dried immediately after cutting-off is very low (18.3 mg/g dry matter), and compared to this the strong water-deficit lasting for 2 days after the water-absorption, i. e. the live-wilting, gave the greatest change, as the total amino acid content increased to 81.5 mg (4.45 times that of the fresh control). The water-treated and live-wilted variant is a control compared to the variants treated with the active substances, and if the IAA solution absorbed variant is compared to this it may be stated that its total amino acid content increased still further, by about 20% (to 97.9 mg).

At the same time, compared to the water-treated control, the total amino acid content did not change significantly on the action of ABA, IAA + GA₃ + FAP and IAA + GA₃ + FAP + ABA treatments: 83.2, 81.8 and 82.7 mg/g, respectively.

It may be concluded from the results that the effect of IAA in increasing the amino acid synthesis and accumulation, on the occasion of the water-deficit of the isolated shoots, is cancelled out by the GA₃, the FAP and the ABA jointly. At the same time, however, the shoots treated with ABA and with ABA + IAA + GA₃ + FAP absorbed approximately 30% less liquid during the 24-hour illumination; as demonstrated by the microscopic examinations, this was induced by the ABA bringing about complete closure of the stomata. The closure of the stomata on the action of ABA was not antagonized by the joint effect of IAA, GA₃ and FAP either. The same

finding was made by TUCKER and MANSFIELD (1971), but they did not investigate the amino acid changes.

The first part (A) of our experiments has two main results: (i) at the time of a water-deficit, a solution of exogenous IAA with a concentration of 20 mg/l increases the total amount of free amino acids accumulating considerably (by 20%); (ii) an ABA solution containing 5 mg/l decreases the water-uptake of the shoots by about 30%, by closing the stomata, thereby reducing the transpiration.

(B) Second part of the experiments involving absorption of the active substances and live-wilting

In the second absorption experiment, besides pure solutions of IAA and ABA, the joint effect of the two active substances is also studied, with the idea that the IAA may increase the accumulation of free amino acids to an even higher level in the live-wilting via the transpiration-decreasing effect of the ABA. The water household and dry weight data and the soluble total protein contents are listed in Table 1.

It can be seen from Table 1 that, as a result of the exogenous ABA, the shoots absorbed nearly 30 ml less water in one day than the control immersed in water, or

Table 1. Effects of IAA, ABA and IAA+ABA on the water balance, dry weight and soluble total protein content of isolated lucerne shoots in the event of a strong water-deficit. Absorption of water or of solutions of biologically-active substances lasted for 24 hours, and the water-deficit for the next 2 days (in air at 20 °C, with a relative humidity of 60% and under an illumination of 3000 lux).

Treatment of isolated lucerne shoots	100 g shoots (fresh weight)				Soluble total protein, mg/g live weight
	Amount absorbed in 1 day from water or solution, g	Amount bound in 1 day from water or solution, g	Weight after 2 days' live-wilting, g	Dry weight after 2 days' live-wilting, g	
Fixed immediately on cutting-off (control)	—	—	—	22,6	25,7
Absorbed with water for 1 day, then live-wilted	121,3	12,5	43,2	22,3	24,9
Absorbed with ABA solution (5 mg/l) for 1 day, then live-wilted for 2 days	83,8	15,1	47,5	22,6	25,2
Absorbed with IAA solution (20 mg/l) for 1 day, then live-wilted for 2 days	112,7	15,4	46,7	22,4	24,8
Absorbed with ABA + IAA solution (5 + 20 mg/l) for 1 day, then live-wilted for 2 days	82,0	15,5	47,9	22,7	25,6

the shoots treated with exogenous IAA. At the same time, as regards the amount of water bound the differences are not large. At any event, the essential fact is that the IAA administered together with the ABA did not cancel out the significant effect of ABA in reducing the water turnover when applied alone.

It may also be stated from Table 1 that the dry weight and soluble total protein content of the isolated lucerne shoots treated with the active substances did not display a characteristic difference compared to the (fresh) control fixed and dried immediately after the cutting-off. It may further be established from the Table that the protein content of the shoots does not change essentially either during the live-wilting if the photosynthesis is active in the incubation period, or the isolated shoots possess a satisfactory carbohydrate basis. The illumination and functioning photosynthesis are therefore very important factors in the course of live-wilting (PÁLFI et al., 1974ab, 1975ab).

A paper chromatogram developed with isatin, which forms the basis of the colorimetric determination of proline, is illustrated in Fig. 2. The isatin reagent reacts extremely sensitively with proline to give a dark blue colour, whereas with other amino acids it gives only pale pink or reddish-brown spots, and accordingly these latter have been encircled.

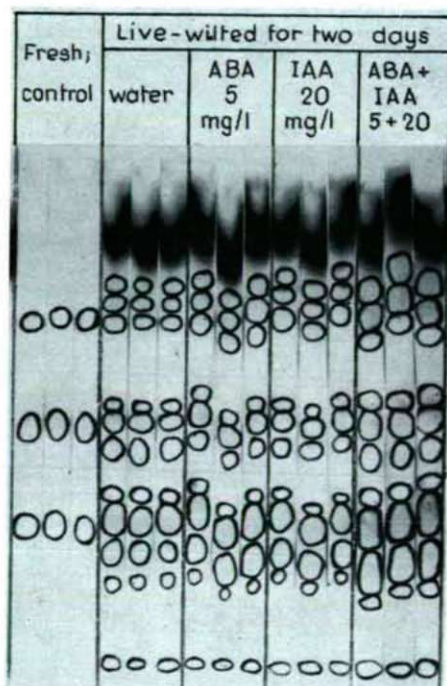


Fig. 2. Changes in the free amino acid composition of isolated lucerne shoots as a result of absorption of water or active substances and strong water-loss (live-wilting) for 2 days. An ascending one-dimensional paper-chromatogram, run in phenol-water solvent and developed with isatin reagent, for elution and colorimetric measurement of proline (every variant run in triplicate, or in 3 bands).

It emerges from Fig. 2 that free proline can be detected only in traces in well-watered shoots which were fixed and dried immediately after isolation (fresh control). At the same time, the proline has accumulated to an extremely large extent in shoots exposed to a strong water-loss (live-wilted) for 2 days. The colorimetric data showed that, of the four variants, the ABA + IAA treatment gave the highest proline content; the absorption treatment with IAA gave a value close to this, but somewhat lower.

Figure 2 indicates that the total amino acid content of (fresh control) shoots fixed immediately after cutting-off is very slight, and that, as regards the water-loss variants, the shoots treated with ABA + IAA gave the largest and darkest spots, i. e. the total amino acid concentration of this variant was the highest.

In the course of the experiments, a detailed analysis was also carried out on the amino acids. The results are presented in Table 2.

It can be seen in Table 2 that as a consequence of the strong water-loss for 2 days (live-wilting under illumination) the total amino acid content of the shoots saturated

Table 2. Changes in the free amino acid content of isolated lucerne shoots as a result of exogenous ABA, IAA and IAA + ABA solutions, and a strong water-loss (live-wilting) for 2 days. Detailed amino acid composition.

Abbreviation for amino acid (+ = indispensable)	Dried on cutting-off (fresh control)	Dried after 2 days' live-wilting			
		Water	Active substances, mg/l		
			A B A 5	I E S 20	ABA + IES 5 + 20
mg/g dry matter					
Asp	0,61	1,46	1,52	1,55	2,15
Thr +	0,63	2,81	2,26	2,31	3,02
Ser	1,72	4,77	5,63	4,83	4,81
Asn	5,31	18,28	18,80	20,32	37,87
Gln	1,65	4,52	4,50	5,61	6,70
Pro	0,40	15,03	14,11	18,14	20,68
Glu	0,82	1,54	1,58	1,46	1,83
- Amb	0,10	0,35	0,47	0,51	0,62
Gly	0,26	0,41	0,40	0,47	0,56
Ala	2,56	4,02	4,71	6,10	5,04
Val +	0,77	3,37	3,52	5,42	5,38
Cys	0,09	0,13	0,25	0,20	0,16
Met +	0,12	0,63	0,68	1,17	1,03
Ile +	0,64	2,64	2,73	3,14	5,87
Leu +	1,02	3,50	3,69	4,21	6,89
Tyr	0,51	1,13	1,02	0,98	2,10
Phe +	0,65	2,52	2,70	3,19	4,75
Trp +	0,42	0,90	0,91	1,86	1,64
Lys +	0,54	1,64	1,67	1,82	1,73
His +	0,20	1,81	1,74	2,43	2,22
Arg +	0,68	1,44	1,50	1,65	2,26
Total aminoacid, mg/g	19,70	72,90	74,39	87,37	117,31
As a percentage of the dry matter	1,97	7,29	7,44	8,74	11,73

The error is less than $\pm 5\%$.

with water after the isolation increased to 3.70 times that of the freshly-fixed control. From this fact it may again be stated that the most significant change in our experiment was in the total amount of amino acids forming and accumulating at the time of a strong water-deficit (including the amounts of proline and asparagine).

In the treatment of absorption with water, the greatest increase was found for proline, which rose in amount to 37 times that for the freshly-fixed shoots. Naturally, the lucerne exhibited a proline type now too, since the strong water-loss caused the proline in the shoots to increase above 1.0% in every live-wilted variant. As found by both ourselves and others, the accumulation of a larger quantity of proline promotes the tolerance of the water-deficit in mesophytic, soft-stemmed plants (KUDREV and TYANKOVA, 1966; PÁLFI, 1968ab, 1969; LEWITT, 1972; VALLEE, 1973; HUBER, 1974; PERDRIZET, 1974; WALDREN and TEARE, 1974; BATES et al., 1975; MELIN, 1975; etc.).

In the shoots absorbed with water and live-wilted there is also a very considerable accumulation of asparagine; although this increased to be only 3.4 times the asparagine content of the (control) variant fixed immediately after the cutting-off, in absolute terms it exceeded even the proline. It appears that, in the even of a water-deficit, lucerne is not only of proline-accumulating type, but also of asparagine-accumulating type. This conclusion was reached by IZMAYLOV et al. (1974) too.

Besides the proline and asparagine, however, the concentration of the essential amino acids also increases considerably as a result of live-wilting, in comparison with the (fresh control) variant fixed immediately after cutting-off: e. g. in the shoots absorbed with water the 2-day strong water-deficit led to an increase of 4 times in the threonine, valine, isoleucine and phenylalanine, an increase of 5 times in the methionine, an increase of 3 times in the leucine and lysine, an increase of 2 times in the tryptophan and arginine, and an increase of 9 times in the histidine.

Since we primarily wished to determine whether the biologically-active substances applied lead to changes in the composition and total amount of the amino acids formed as a result of the live-wilting of the shoots under illumination, in the following the results are referred not to the variant fixed immediately after cutting-off, but to the variant saturated with water for 1 day and subsequently live-wilted for 2 days.

From the total amino acid quantities in Table 2 it can immediately be established that the exogenous active substances changed the amino acid picture of the (control) variant treated only with water and then subjected to a strong water-loss for 2 days. The IAA treatment and the IAA+ABA combination increased the total amount of amino acids by 19% and 60%, respectively, compared to the water-treated control. At the same time, the ABA treatment in itself did not result in a characteristic amino acid change. Our assumption was therefore confirmed: the ABA retained its water turnover (transpiration)-decreasing effect even when combined with IAA, and in addition (or even thereby) elevated the amino acid-increasing effect of IAA by a factor of 3, from 19% to 60%.

Table 2 also shows that the combined ABA+IAA treatment led to a significant increase in the concentration of the amides, proline and the essential amino acids, compared to the water-treated shoots; as regards the protein synthesis, therefore, the amino acid composition improved further. It may be seen from the data that ABA applied alone did not produce an appreciable change, either qualitatively or quantitatively, in the amino acid metabolism level; it therefore acted by another route or

directly on the water turnover (e. g. by closing the stomata). This conclusion was also reached by Mittelheuser and Van STEVENINCK (1969), TUCKER and MANSFIELD (1971), KRIEDEMANN et al. (1972) and LEWITT (1972).

Discussion

In our previous work (PÁLFI, 1971; PÁLFI et al., 1972, 1973, 1974, 1975) it was found that the increase of the total free amino acid content of the shoots and leaves isolated from greenstuffs and green fodder is generally of different extents in the course of live-wilting, depending on whether or not the species in question is of proline-accumulating type. With the method of artificial live-wilting, the protein-forming total amino acid content of species of proline type (e. g. lucerne, clover, pea, wheat, savoy cabbage) can be increased to 7—11% of the dry matter. At the same time, the total amino acid concentration of species of non-proline type (e. g. spinach, lettuce, maize, bean, white lupine) generally attains a somewhat lower level, 5—8%, in the course of live-wilting under illumination.

The higher total amino acid accumulation of the species of proline type originates primarily from the large amount of proline itself, this generally being accompanied by a considerable asparagine concentration increase too, particularly in the Leguminosae family species of proline type. Live-wilting does not lead to a significant difference in general between the species belonging to the two types, as regards the appreciable increase in the total amount of essential amino acids (PÁLFI et al., 1974, 1975).

The total amino acid level and the qualitative composition attainable during live-wilting depend on many other endogenous and exogenous factors in addition to whether the given plant species is of proline type or not.

A factor which may be regarded as endogenous is the selection of the appropriate varieties within the species in question, and the selection of the various developmental phases of the plant. It seems that optimum choice and adjustment of the exogenous factors are both of very great importance. In addition, it must also be taken into consideration that a change in the value of some exogenous factor may lead to subsequent changes in the levels of the other exogenous effects.

As regards the exogenous conditions, stress must primarily be laid on the importance of the fact that the plants destined for live-wilting should be field-grown under optimum conditions. This ensures a favourable physiological state of the isolated shoots. During the pre-growing, the provision of the plants with a good supply of water, nitrogen and other nutrients is in particular indispensable. It is also essential that the weather for 4—5 days prior to the cutting-off of the shoots should also be relatively favourable: it should be sufficiently warm, and the plants should receive several hours of sunlight daily. In this case, the shoots possess a satisfactory carbohydrate reserve during the live-wilting, and thus "protein respiration" does not occur. If the nitrogen supply of the plants is not certainly favourable, a plant nutrient spray may be applied too 2—3 days before the shoots are cut off.

The season in which the individual plant varieties are grown is also of importance. For example, as a result of live-wilting, spring spinach always accumulates more total amino acid than any variety sown in autumn. Greenhouse-grown spinach, however,

gives a very poor result. Lucerne and savoy cabbage harvested in the summer provide a better starting basis than those harvested in the autumn.

During live-wilting it is most important to regulate the following exogenous factors: the air temperature; its relative humidity; its carbon dioxide content; the nature and intensity of the illumination; the duration of live-wilting; and the rate and extent of loss of water of the isolated shoots. On attainment of the optimum duration of live-wilting, the shoots must immediately be fixed at 70 °C and dried, as protein loss will occur in subsequent live-wilting.

The fact that fairly different levels of amino acid accumulation were obtained in the live-wilting of a given plant species and variety is attributed to the varying conditions of pre-growing, and to the variations in the exogenous factors of live-wilting. This is not only characteristic for the results of our earlier work (PÁLFI *et al.*, 1972, 1974, 1975), but also emerges from the two parts (sections IIIA and IIIB) of our present experiment.

As regards the amounts of total amino acid accumulating during live-wilting, however, the differences due to the environmental conditions are not completely extreme: in the case of greenstuffs such as spinach and savoy cabbage, we ourselves did not grow the starting raw material in even a single case, but obtained it commercially, and accordingly, as a rule, neither the variety of the plant, nor its site of growth, and indeed in many cases the exact time of harvesting, was not known. Nevertheless, in the live-wilting of these isolated leaves fairly uniform total amino acid accumulation results were achieved (PÁLFI, 1971; PÁLFI *et al.*, 1972).

In further of our experiments (PÁLFI *et al.*, 1975), physiological factors were sought, the application of which led to a further enhancement of the total amino acid accumulation in the course of live-wilting. We set out from the fact that the endogenous ABA content of the isolated leaves is elevated to 10–40 times the normal level as a result of a water-deficiency persisting for some hours (WRIGHT, 1969; ZEEVAART, 1971; KRIEDEMANN *et al.*, 1972). At the same time, as a consequence of an increasing water-deficit, the concentrations of IAA and other growth substances decrease rapidly (DARBYSHIRE, 1971; ITAI and VAADIA, 1971).

The data of ASPINALL *et al.* (1973), BATES *et al.* (1973), HUBER (1974) and KANG and STANLEY (1971) indicate that there is a correlation between the activity changes of the individual growth substances, the accumulation of the amino acids and the water-household of the plants, and the endurance of the water-deficit.

It can be seen from all these data that the biologically-active substances play a regulatory role as regards the amino acid and protein metabolisms in the course of the water-loss and live-wilting of the isolated shoots. Positive results as regards the magnitude of the accumulation of amino acids were achieved earlier in live-wilting experiments, by the application of certain growth substances exogenously (PÁLFI *et al.*, 1975).

The present experimental results show that exogenous IAA or combined IAA + ABA treatment during the live-wilting of isolated lucerne shoots leads to an enhancement of the accumulation of protein-forming amino acids by a further 20–60%, without an accompanying substantial decrease in the protein content, if the shoots possess a satisfactory carbohydrate reserve (under illumination). At the same time, compared to the levels for the water-treated control, the total amino acid values of the isolated shoots were not increased during live-wilting by treatment with ABA alone, or by the combination ABA + IAA + GA₃ + FAP. The ABA treatment decre-

ased the water-turnover of the shoots by 30%, by closing the stomata, and this effect was not antagonized by the joint effect of IAA, GA₃ and FAP.

In the evaluation, attention must be paid to the fact that the total amino acid content of the shoots fixed and dried immediately after cutting-off (fresh control) is very low; for instance, in part (A) of our experiment it was 18.3 mg/g dry matter. The largest change compared to this was given by the strong water-deficit for 2 days, i. e. live-wilting, since the total amino acid content then rose to 81.5 mg/g dry matter, 4.45 times the value for the fresh control. This is at present the highest free amino acid production attainable by biological means.

The amino acids necessary for the building-up of the proteins in the organisms of animals and man are mainly taken up in the form "bound" into proteins. However, hydrolytic splitting of the proteins, i. e. digestion, is accompanied by a significant protein loss.

According to the data processed by SZLAMENICZKY (1972), for all the animal species in Hungary the total amount of digestible protein in the fodders used yields on average only 18—19% animal protein. This means that not even one-fifth of the protein content of the fodders undergoes protein-utilization. In contrast, the free protein-building amino acids of plants are absorbed to an extent of 98%, i. e. almost totally (RIGÓ, 1976).

In exact human nutritional examinations (RIGÓ, 1976), it emerged that the digestibility quotient for an amino acid mixture is 98, while that for proteins is only 37; in enteritic children the protein-utilization as regards the free amino acids is 90, whereas that for proteins is only 26. Feeding with free amino acids is therefore of great importance in connection with dietetics too. BARNÁ et al. (1976ab) report that the utilization of amino acids in healthy individuals is more advantageous than that of proteins; the digestibility quotient, the biological value and the protein-utilization uniformly exhibit higher values. RIGÓ assumes that our foods will be subjected to new judgement from the aspect of the variations in the free amino acid content.

As found by THOMAS (1973), the value of lucerne is increased by the fact that it may also be used for human feeding. In many states in the USA, lucerne is already sold in the form of large tablets in numerous stores, and recipes have been developed for the preparation of bread and other foods. Thomas reports that the experience to date shows that lucerne is a very effective nutrient, with which many pathological physiological lesions too may be treated. In addition, lucerne is an important constituent of baby foods.

We too consider that young lucerne shoots, carefully dried at 70°C and granulated, and possessing an elevated amino acid content as a result of this live-wilting, could form a sure protein basis in the feeding of populations in protein-poor countries. In Hungary a small group has been regularly consuming green-vegetable foods prepared from live-wilted lucerne or a powdered lucerne and spinach mixture (flavoured in various ways) for 3 years.

At present, as RIGÓ (1976) too concludes, encouraging methods for the future are the production of free amino acids with yeasts, the production of amino acids from side-products of the petrochemical industry with pure cultures of bacteria, and the accumulation of the amino acids in isolated leaves.

We have established that an extract can be obtained from lucerne or savoy cabbage by simple boiling with water, the amino acid content of which is enriched to 8—10% of the dry matter by live-wilting, and that a concentrate containing 40—50%

amino acid can be prepared from this by evaporation. At present the live-wilting of isolated shoots and leaves is the most simply performable procedure, and therefore the cheapest method for the production of natural amino acid mixtures by biological means.

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STUDIES OF HERBICIDE SENSITIVITY IN THE UPTAKE OF DIFFERENT IONS BY RICE ROOTS

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Abstract

A study was made of the effect of SYNPRAN 111 herbicide on the uptakes of potassium, phosphate, nitrate and ammonium ions by rice roots. The isotopically-labelled uptake solution contained different concentrations of SYNPRAN 111, which is 30,6% 3,4-dichloropropionanilide + 8,0% 2, 4, 5-trichlorophenoxyacetic acid amyl ester. It was proved that at 10^{-4} M herbicide concentration potassium and nitrate ion uptakes were at first effectively inhibited, while on 10^{-6} M herbicide treatment the effects were not injurious, but rather favourable. In general it can be stated that potassium and nitrate nitrogen uptakes are more sensitive towards herbicide treatment than phosphate or ammonium nitrogen uptakes. The toxic or stimulatory effect of SYNPRAN 111, however, was also notably influenced by the concentration and temperature of the uptake solution, showing the importance of environmental factors in herbicide action.

Introduction

It has long been well known that ion uptake by plants is fairly strongly influenced by some environmental factors, e.g. temperature, pH, aerobic or anaerobic conditions, etc. (FRIED et al. 1965, LEWIS-WORKMAN 1964, SUTCLIFFE 1962, ZSOLDOS 1967, 1972). Recently it was also established that some practically-employed, biologically-active substances, e. g. herbicides, fungicides, etc., similarly have effects on the ion uptakes and mineral nutritions of plants. From the literature data it is clear that the concentration of the herbicide or fungicide plays a very important role in its effect. In general, treatment with higher herbicide concentrations is toxic, whereas a low concentration very often has a favourable effect (CHESALIN-TIMOFEJEVA 1968, FREAR-SHIMABUKURO 1970, HAUNOLD-ZSOLDOS 1976, MORELAND 1967, ZSOLDOS 1974). The investigations further indicate that several compounds may help to produce not only a higher yield, but a better quality too (IRRI Ann. Rep. 1970—1972, JAISWAL et al. 1973).

Recently it was proved that the effects of herbicides are likewise considerably influenced by certain environmental factors, e. g. temperature, nutrient concentration, etc. The experimental results similarly show that ion transport responds differently towards herbicide treatment (HAUNOLD-ZSOLDOS 1976, HILTON-JANSEN 1963, NODABARAKI 1968).

From the above literature data it is clear that herbicides and fungicides not only control weeds and blights, but can also modify the mineral nutrition and in this way the yields of plants. As different biologically-active compounds are widely employed in agriculture, we feel that special attention must be paid to this double effect of

herbicides in the future. For this reason, ion uptake experiments have been carried out with different ions to examine the effects of herbicide treatment and some environmental factors.

Materials and Methods

The potassium, phosphate, nitrate and ammonium ion uptakes of excised rice roots (*Oryza sativa* L. cv. Dungha Shali) were investigated at different concentrations of SYNPRAN 111 herbicide. Seeds were disinfected, rinsed in running tap water for 6 hours, and allowed to germinate on filter paper in Petri dishes. The seedlings were grown under standard conditions as described earlier (ZSÓLDOS 1972, 1974).

6–8-day-old plants were used in the further experiments, their roots then being about 7–8 cm long. Before the start of a short-time ion uptake experiment, the roots were excised and immediately washed for 10 minutes in distilled water. The samples were then placed in 500 ml aerated, isotopically-labelled uptake solution containing different concentrations of SYNPRAN 111 (a product of the Budapest Chemical Works, Hungary), which is 3, 4-dichloropropionanilide (30.6%) and the amyl ester of 2, 4, 5-trichlorophenoxy-acetic acid (8.0%). In the following, the concentration values given refer to the pure active ingredient.

The potassium uptake studies were carried out in 10^{-3} M $K(^{86}Rb)Cl + 5 \times 10^{-4}$ M $CaSO_4$ solution. The phosphate ion uptake was studied from 10^{-4} M or 10^{-3} M $KH_2^{32}PO_4$ solution, the isotope contents of experimental material being measured with a scintillation counter. The uptakes of nitrate and ammonium ions from 10^{-3} M NH_4NO_3 or $NaNO_3$ solution were studied with the help of ^{15}N , using a mass-spectrometer for the determination of nitrogen uptake as described earlier by PROKSCH (1969).

The ^{15}N concentration of the $^{15}NH_4NO_3$ was 70 atom per cent, and of the $Na^{15}NO_3$ was 95 atom per cent (a product of the VEB Berlin Chemie). The pH of the uptake solution was adjusted to 6.5 and was checked again after the incubation. The root samples were removed from the solution after a one-hour or 80-min uptake period, and were washed three times for one minute. The isotope contents of the samples were measured as mentioned above. The results are given in μ mole ion uptake/g dry weight or atom % ^{15}N excess as a percentage of the control (untreated). Data are means of three replications in all the experiments.

Results and discussion

1. Uptakes of different ions: The potassium, phosphate, nitrate and ammonium ion uptakes characteristic of herbicide treatment at different concentrations are visible in the graphs of Fig. 1 and 2. The experimental results clearly indicate that potassium and nitrate ions were more sensitive towards SYNPRAN 111 herbicide treatment than phosphate or ammonium ions.

In connection with the nitrogen uptake, it is noteworthy that the ammonium ion is taken up 8–10 times faster than the nitrate ion. As to the K ion uptake the absorption rate of potassium is about 7 times as great as that of phosphate ion.

From the data it can also be seen that at lower herbicide concentration there is a slight stimulatory effect too (except for the phosphate ion). Although the differences between the ion uptakes of the control (untreated) and the herbicide-treated samples are not very large, they are reproducible. At a SYNPRAN 111 concentration of 10^{-5} M a slight inhibitory effect can be observed (except for the ammonium ion), while at 10^{-3} M the active ion uptake practically ceases.

These data unambiguously confirm that, although the effects of the herbicide are considerably influenced by its concentration, the sensitivities of different ions to the herbicide treatment vary appreciably. In our opinion these experimental results

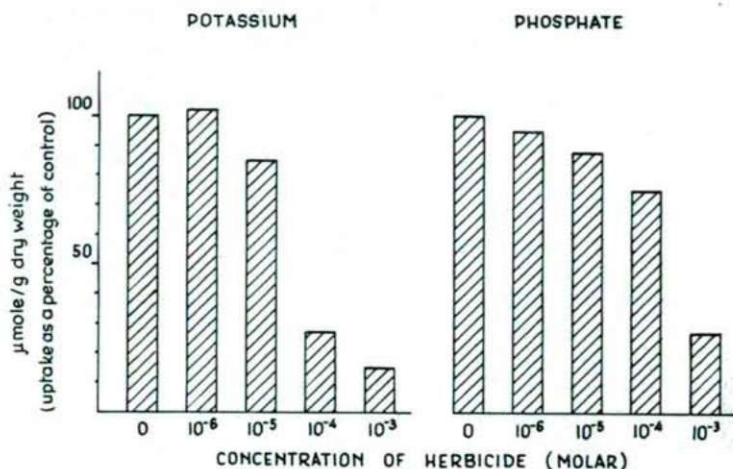


Fig. 1. The effects of different herbicide concentrations on the uptakes of potassium from 10^{-3} M KCl solution and phosphate from 10^{-3} M KH_2PO_4 solution by rice roots. Uptake time: 60 minutes.

show, among others, the practical importance of such an investigation, as the toxic or enhancing effect of herbicides on ion uptake and mineral nutrition, as already mentioned, can also modify the yields of plants.

2. Influence of some environmental factors on the effect of herbicide treatment. As seen in Fig. 3, the effect of herbicide treatment on the ion uptake varies to a certain extent with the concentration and temperature of the uptake solu-

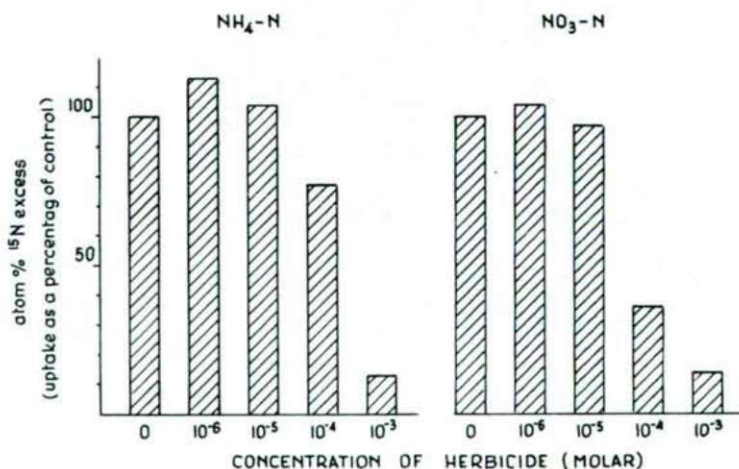


Fig. 2. The effects of different herbicide concentrations on the uptakes of ammonium from 10^{-3} M NH_4NO_3 solution and nitrate from 10^{-3} M NaNO_3 solution by rice roots. Uptake time: 80 minutes.

tion. The experimental data show that at lower herbicide concentrations a slight stimulatory effect is found with 10^{-4} M uptake solution for phosphate too, whereas such an effect is not detectable with 10^{-3} M uptake solution.

These results are rather surprising, especially if we consider the two mechanisms of ion uptake described earlier (EPSTEIN 1972).

Similarly noteworthy effects are induced by lower and higher temperatures, as revealed by the graphs of Fig. 3. The experimental data clearly indicate that at lower temperature the SYNPRAN 111 herbicide has a stronger effect on the ion uptake than at 30°C . It is worth mentioning that, for example, in the case of wheat under these experimental conditions the temperature effects are just opposite to those for rice (unpublished data). This is not so surprising, however, if we think of the difference between the ion uptakes of thermophilic (rice) and non-thermophilic (wheat) plants (ZSOLDOS, 1972).

Low temperature in itself has an unfavourable effect on the ion uptake as well known from our earlier experimental data (ZSOLDOS 1972): The total ion uptake is naturally always significantly higher at 30°C than at 14°C . In our case the difference is about 50 per cent.

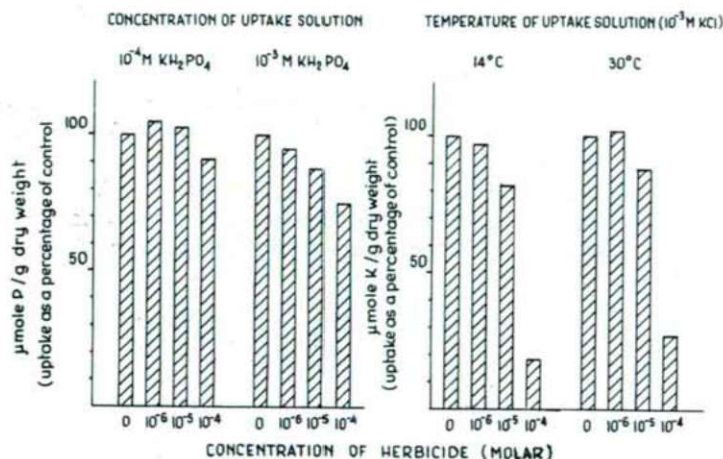


Fig. 3. The effects of the concentration and temperature of the uptake solution on the phosphate and potassium ion uptakes during different herbicide treatments. Uptake time: 60 minutes.

To summarize, it is seen from the above data that the well-known classical environmental factors, e.g. temperature and nutrition concentration, could have special effects on the mineral nutrition of herbicide-treated plants. It is obvious, therefore, that close attention must be paid to the interaction which exists between mineral nutrition, herbicide treatment and some environmental factors. These must be taken into consideration in practice too, before or during herbicide treatment, and on the use of fertilizers.

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INDOLE HYDROXYLATION OF THE MEMBERS OF THE COMMELINACEAE FAMILY

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(Received December 10, 1976)

Abstract

It can be ascertained from our experiments that at eight members of the Commelinaceae family the 5- and 6-OH-indole derivatives were produced. A difference manifested itself in the quantities of the hydroxy-indole derivatives produced.

Introduction

In the process of hydroxylation, the reactions were studied by us by means of indole transformation because the compounds of indole structure are of very considerable importance in metabolism and in the constitution of organism. We have also determined the quantity of the indole-hydroxy derivatives produced in the same manner as in literature when the endogenous indole was isolated from maize seedlings and also purified (REVIN, 1971). On the basis of the indole-hydroxy derivatives it may perhaps be possible that the members of a plant family can be separated by means of the quality of derivatives and, possibly, Phylogenetic connections can also be established. In another domain of problems, the developmental phases of seedlings could be separated by means of the hydroxy derivatives of anthranilic acid (MATKOVICS *et. al.*, 1972).

Materials and Methods

Our experiments were performed with the leaf and stem samples of the following members of Commelinaceae family: *TRADESCANTIA ALBIFLORA* BRÜCKN. (syn., *Tradescantia viridis* hort., *Tradescantia venezuelensis*, *Tradescantia fluminensis* VELL. em. BRÜCKN., *Tradescantia blossfeldiana* MILDBR., *Tradescantia sillamontana*, *Zebrina purpurea* BRÜCKN., *Seterasia purpurea* BOOM.).

We have investigated into the indole hydroxylating capacity of the tissue of leaves and the tissues of stem, according to the following method: The indole (1000 γ /10 ml) was dissolved in a 6 pH phosphate buffer, weakly warmed over a water bath. One g fresh vegetable tissue, leaf or stem was cut in 3—4 mm straks and infiltrated for 3 minutes. After being infiltrated, the vegetable parts were dried in room air and 1 g matter was homogenized in a 10 ml indolic buffer. The homogenizate was incubated at room temperature for five hours, then the system was stopped with ether. After ethereal precipitation and distillation, the dry remainder was dissolved in 1 ml ether, and — with a papillary tube made of Pasteur's pipette — it was applied on a Kieselgel — G 10 \times 20 cm plate, plated in a benzol-acetone mixture (90:10). After 30 to 40 min. plating, the front-line was indicated, and, after blowing on it warm air, we developed it with van Urk's reagent. The chromatogram, after standing for twelve hours, was photographed, and drawn, and the Rf. values were calculated. The spots were scraped off and dissolved in 5 ml ethanol, then — after being dissolved for two hours —

they were centrifuged and — against the supernatant ethanol — measured at 540 mmikron wavelength. On the basis of the calibration curve, the indole quantity of the indole derivatives and the remainder was determined for γ/g fresh weight. The identification of derivatives took place by reason of Fenton—Cier's system (Eich-Rochelmeyer, 1966).

Discussion of the experimental results

We have investigated into the hydroxylating capacity of eight members of the Commelinaceae family. The behaviour of leaves and stem was followed with particular attention because even the leaves of *Tradescantia* are able to regenerate roots (HORVÁTH—KOVÁCS, 1969). The general multiplication takes place with leafy shoots although root and shoot can be regenerated by the stem without leaves, too. The separate investigations into both organs are justified by this. In the Table, the quantity of derivatives coming about on the carbon atoms 5 and 6 is shown. In another situation, the hydroxylation could not be demonstrated at these plants, resp. plant-parts.

In the Table, the average values of eight repetitions are shown. It is to be established that the leaves and stems of the eight kinds of *Tradescantia* behaved in the same way, on the basis of the produced quantity of 5—OH and 6—OH indoles. We could not establish any difference between the members of the Commelinaceae family, at the indole-hydroxylation.

In the chromatograms, we are demonstrating the derivatives produced in the leaf of *Zebrina pendula* SCHNIZL. and FENTON—CIER's comparative system.

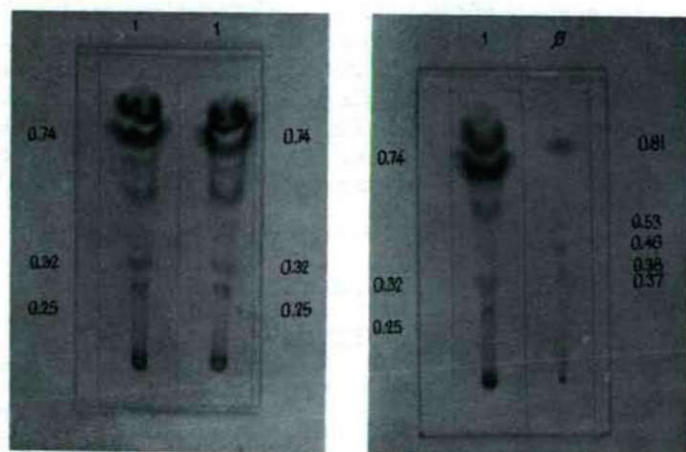


Fig. 1. Chromatogram and Rf values of the indole-hydroxy derivatives produced in the leaf of *Zebrina pendula* Schnizl (1, 1, 1) and of Fenton—Cier's system.

At marks 1—1—1 the quantities produced in leaves can be seen. The 0.32 Rf values of 6—OH, the 0.25 Rf values of 5—OH are indicating the uniformity of our experiments at the three repetitions shown here, as well. The Rf value of the remaining indole is also identical in all the three cases, 0.74. By the Rf values of FENTON—CIER's system (under mark F) the reliability of the evaluation may also be supported.

Table 1. Quantity of the indole-hydroxy derivatives of genus *Tradescantia*, reckoned γ /g fresh weight

Species	5—OH—indole		6—OH—indole	
	leaf	stem	leaf	stem
<i>Tradescantia albiflora</i>	1.45	2.35	1.70	2.30
<i>Tradescantia venezuelensis</i>	2.05	2.10	2.70	2.55
<i>Tradescantia fluminensis</i>	2.55	3.65	3.10	3.10
<i>Tradescantia blossfeldiana</i>	2.30	1.55	2.85	2.75
<i>Tradescantia sillamontana</i>	2.05	2.25	1.60	1.60
<i>Zebrina pendula</i>	1.75	1.85	2.15	2.55
<i>Zebrina purpusii</i>	2.10	1.95	2.1	2.05
<i>Seterasia purpurea</i>	1.60	1.30	2.00	1.55

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EFFECT OF HERBICIDES OF 2,4-D BASE ON WATER-PLANTS

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Abstract

The destructive effect of 2,4-D induces in the cells of water-plants essentially different changes in the enzyme level from the mechanical impact or the pathogenic infection. The indole-inductivity of 2,4-D has a much more considerable influence on promoting the formation of new indole-derivatives than the indole-content of the experimental medium. In some water-plant species the 2,4-D-induced formation of the indole-derivatives may come about through the reversibility of the reaction way shikimic acid — IAA.

Introduction

The investigation into the effect of plant-protecting agents on some components and members of the living world is a real demand of the environmental conservation and as such, it extends primarily over the biotope most endangered by pesticides, the aquatic ecosystems. From among pesticides, first of all herbicides are to be taken into consideration in this respect because the development of these chemical agents is the most dynamic in our days.

A very important group of the hormonal herbicides are formed by phenoxy-alkancarboxylic acids and, within these, by phenoxy-acetic acids and their derivatives. Their most characteristic property is the so-called auxin-effect, similar to growth regulators, its essence being that auxin, which in a weak concentration is able to promote vegetable growth, applied in a strong concentration has a retarding effect. It is, however, made possible by the nearer knowledge of various effects of the auxinic compounds, to apply these compounds not only as herbicides but also as growth regulators. Agents of this character are by and large synthesized in the plants themselves, as well, resp. their formation can be influenced by other substances.

2,4-D, as a lipid-soluble substance, changes even the permeability of the cell-membrane, and under these conditions an increasing efflux can take place, the cytoplasm may outflow through the membrane (Dexter, 1969). As at herbicide treatment the effective agents always get into touch with cell membranes, the phytotoxic effect can be measured well by the change in permeability, as well (ZSOLDOS, 1974).

Materials and Methods

Our experiments were performed on water-plants. *Myriophyllum* sp., applied from June to November, has originated from the main channel of Kőrógyér belonging the irrigation system of the Kurca, while in other months of the year we worked with *Elodea canadensis* grown under artificial

conditions. The experiments were set on through different periods (between 1—35 days), with stock solution of 0.6, 3.0, 6.0, 166.0, 333.0 ppm Dikonirt (Na-salt of 2,4-D). The control was running tap water.

The determination of the peroxidase enzyme was performed by applying guaiacol reagent with spectrophotometric method, and that of indole-hydroxylation with thin-layer chromatography, according to HORVÁTH *et al.* (1975).

Results and their evaluation

It is described by several researchers thus, among others, by FARKAS (1968) that in the tissues resp. cells, damaged mechanically or by a pathogenic infection — like a protective mechanism induced — the quantity of peroxidases and polyphenolic oxidases increases. As the considerable destruction mentioned above is to be attributed to the effect of 2,4—D, exerted on the permeability of the cell-membrane, it seemed to us justified to extend the concept of „cellular injury“ over the impact of chemical agents, as well. In this case, we tried to draw a conclusion from investigating the peroxidase activity concerning the possible connection between the change in the quantity of enzyme and the 2,4—D concentration applied.

In the first part of our investigations into the peroxydase activity, we put *Myriophyllum* sp., developed under natural conditions, into a solution containing 2,4—D. The three treatment concentrations were chosen so that even the lowest dose should be at least one order of magnitude higher than the maximum of the level of the agent remainder, formed in the water as a result of the possible herbicide pollution, lest the herbicide concentration accumulated from the water in the course of years covers up the effect of the treatment dose. The other two concentrations were raised to an extremely high level in order to reveal if a high dose like this can even be taken up by a water-plant at all.

The first destruction took place on the 38th day in the solution of 6 ppm. As our experimental series was intended to be of comparative character as to its effect, as a result of this the further investigations were cancelled. In the water-plants treated with the other two concentrations, like in controls, for a long time there was no physical change. There manifested itself, therefore, an essential difference between the doses for the time being — at least in this respect.

It is to be seen in the figures well that the courses of all the three curves are different. The value of the peroxidase activity, measured as a result of the concentration of 6 ppm, is approximately the same on the first and last days of investigation. It never exceeds control, its changes, in the course of the experimental series, are uniform (Fig. 1).

In the intervals of the activity values of 166 ppm there is a considerable difference between the starting and ending points, the tendency of the curve is rising, it exceeds the value of control only at the endpoint of investigation, and this is, at the same time, its maximum point, as well (Fig. 2).

The activity level of the highest concentration is of declining tendency during the experimental series, exceeding the control similarly only once (what is the maximum point, here too). This takes place immediately after beginning the investigations (Fig. 3).

From among the minimum values of the three curves, those of two, and with a very little difference that of the third, as well, fell to the 24th day. The following

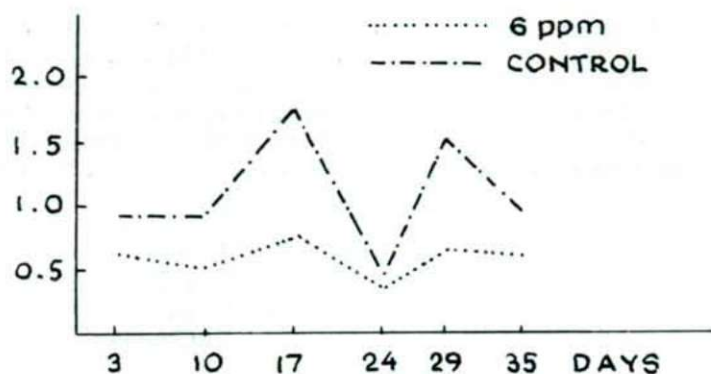


Fig. 1. Effect of a 2,4-D treatment of 6 ppm on the peroxidase activity in *Myriophyllum* sp.

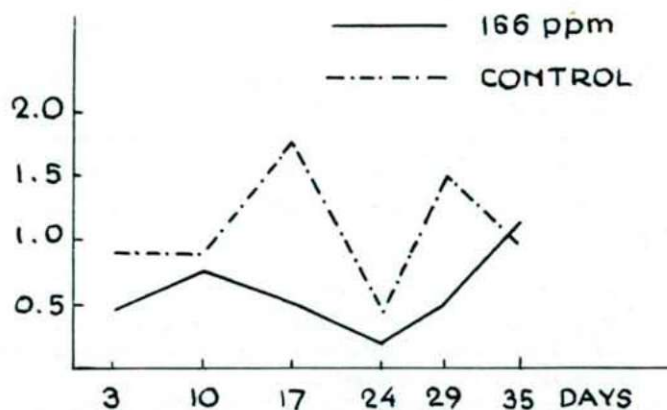


Fig. 2. Effect of a 2,4-D treatment of 166 pm on the perodase activity in *Myriophyllum* sp.

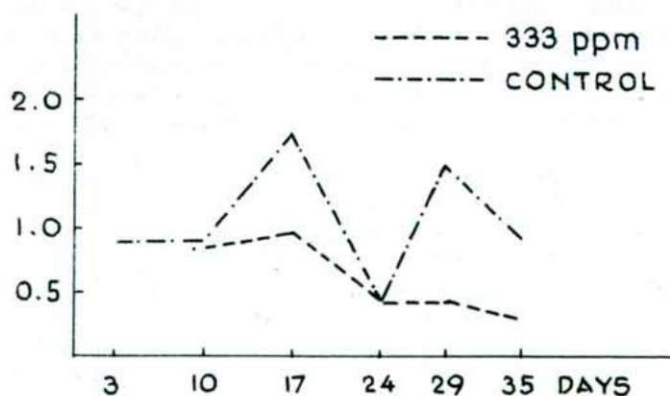


Fig. 3. Effect of a 2,4-D treatment of 333 ppm on the peroxidase activity in *Myriophyllum* sp.

measurements were concentrated, therefore, first into five, later into six days. We could no more return to the original interval because it would have fallen to the 42nd day but on the 38th day — as described before — the concentration of 6 ppm proved to be of destructive effect. We drew the conclusion partly from this, partly from the course of curves that the lowest dose proved to be the most effective. Our hypothesis became confirmed when we plotted the curves in a figure as compared to one another (Fig. 4).

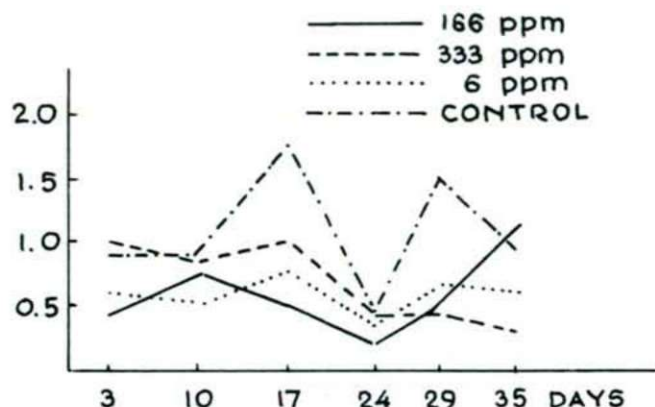


Fig. 4. Effect of 2,4-D treatment of different concentrations on the peroxidase activity in *Myriophyllum* sp.

It is to be seen that the curve of enzyme activity, obtained as a result of the concentration of 6 ppm, is quasi the resultant of the other two, supporting this also by that, in case of higher doses, the herbicide effect develops, as compared with the lowest one, either very early or too late.

Wanting to investigate into the spectrum of the efficient herbicide concentration, in the further part of our experimental series concerning the enzyme activity we have not applied the 2,4-D concentration of 166 and 333 ppm but chose the doses in a way that the lowest 2,4-D concentration, of 6 ppm, which gave the previous most interesting conclusion, should be, this time, the highest one. And two more doses were chosen from a similar, or smaller but one, order of magnitude. For these, however, owing to the water pollution problems outlined above, we have no more applied the test-plant mentioned before but *Elodea canadensis* which was grown under artificial conditions.

We wanted originally to extend the time of the experimental series, in this case too, to the interval used in the preceding but the destruction, similarly in case of the 6 ppm concentration, here already followed on the 19th day. Measurements were extended to the early dates (days 3, 6, 8, etc.), as reckoned from the treatment and compared to the previous 7 days time lag, because we wanted to study the initial stage of the accumulation of the remainder of agents, as well.

It can be read from the figures that in all the three curves the initial and end-points approximately agree but while the levels of the enzyme activity of the 0.6 ppm concentration are showing a strongly upward tendency, almost sine curve-like, exceeding the control values repeatedly and many times (Fig. 5), the values belonging

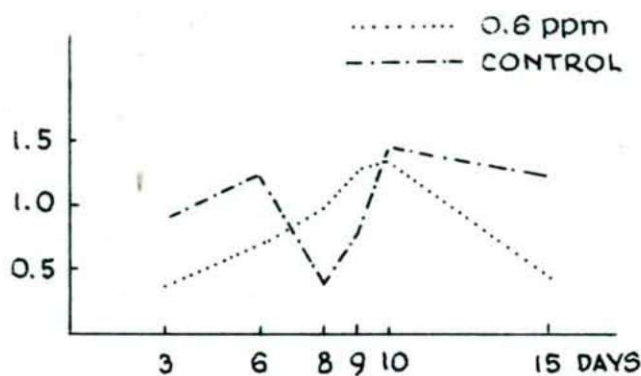


Fig. 5. Effect of 2,4-D treatment of 0.6 ppm on the peroxidase activity in *Elodea canadensis*.

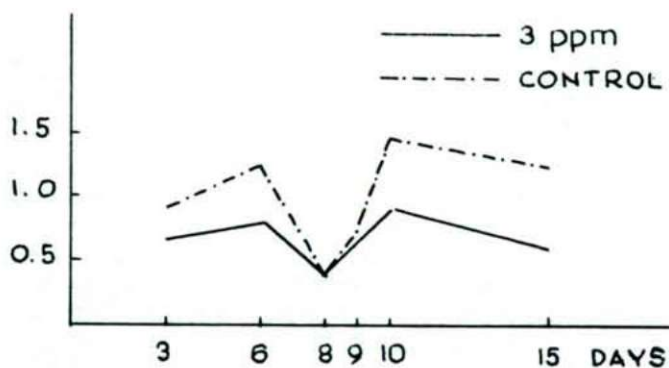


Fig. 6. Effect of 2,4-D treatment of 3 ppm on the peroxidase activity in *Elodea canadensis*.

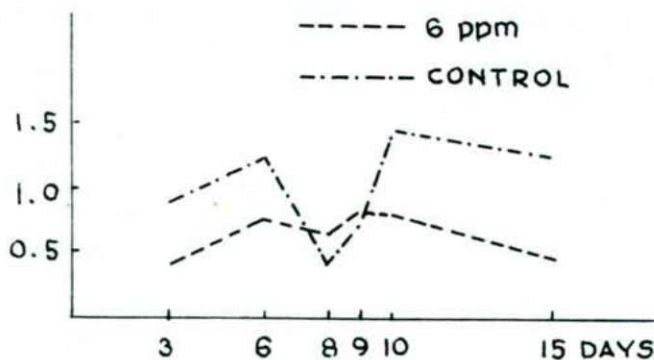


Fig. 7. Effect of 2,4-D treatment of 6 ppm on the peroxidase activity in *Elodea canadensis*.

to 3 ppm have a downward tendency (with a nearly „reversed“ sinus curve character), never exceeding the control level (Fig. 6). The activity values are uniform, in these cases too, only in case of the 6 ppm dose (Fig. 7).

The correctness of our earlier supposition is also verified by plotting the values in a figure (Fig. 8).

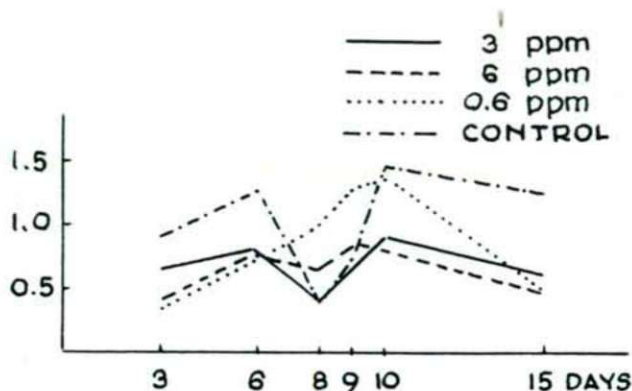


Fig. 8. Effect of 2,4-D treatment of different concentrations on the peroxidase activity in *Elodea canadensis*.

It is apparent that the resultant of curves is given also here by the values of the 6 ppm concentration. In this way, there proved to be most efficient, here too, this dose, increased in the present case by a species-specific factor because the same concentration induced an irreversible physical change in case of *Elodea canadensis*, as compared to the *Myriophyllum* sp., exactly in half as much time.

From the investigations into the peroxidase enzyme activities we could, on the one hand, establish the most efficient herbicide concentration applied, on the other hand, draw the conclusion that the changes of the chemical agent-induced cell "injury" in enzyme level considerably differ from those induced by a mechanical impact or a pathogenic infection.

But by the auxin-like effect of 2,4-D not only the performance of our experimental series was considerably influenced; one of our measuring series, resp. the method used there was made justified decisively by this. In a broader sense, namely, even the compounds may be considered as auxin, which are the precursors of auxin (IAA); thus, among others, the indole itself, by which the heterocyclic basic frame is given. It is known from SÜDI's investigations (1964) that the formation of an inductive IAA precursor, e. g. that of the indole-acetyl-aspartat, can only take place after a pre-treatment with substances of auxinic effect, thus with 2,4-D, resp. as a result of IAA exceeding the physiological concentration. We have wanted to study the effect of the 2,4-D treatment upon the formation of indole and its metabolites, on the basis of these connections.

At first we wanted to determine the indole-derivatives, having existed in water-plants already originally, without any indole induction and then with two kinds of indole administration. Settings were carried out with a middle-long treatment period

and strong 2,4-D concentration. The latter one was performed to establish the extreme limits of doses. As a test-plant, *Elodea canadensis* was applied. This meant an advantage mainly in the indole-infiltration experiments because of its broader leaves.

Table 1. Change in indole derivatives in *Elodea canadensis* as a result of an 8-day herbicide treatment.

Indole-derivatives	2,4-D cc. (ppm)	In phosphate buffer		In indolic buffer		In infiltrated buffer	
		R _f	γ	R _f	γ	R _f	γ
6—OH—indole	0	0,20	2,8	0,19	1,7	0,19	2,5
	6	0,19	2,5	0,19	2,5	0,18	3,5
	166	0,14	2,0	0,14	2,5	0,11	2,8
	333	0,11	2,8	0,16	2,5	0,16	4,0
5—OH—indole	0	—	—	0,32	0,5	0,31	1,8
	6	—	—	0,31	2,0	0,28	2,3
	166	—	—	0,22	1,8	0,20	2,8
	133	—	—	0,28	2,3	0,27	2,5

It may be established from the Table that in water-plants originally there can only be found the 6—OH—Indole while the 5—OH—Indole is produced by induction. The difference seen between the two kinds of indole induction is first of all that the quantity in weight of both derivatives is somewhat increased by being infiltrated; at the same time, the R_f values are a little decreased. The phenomenon may supposedly be attributed to that, in case of identical compounds, the spot of a higher „material content“ runs up with more difficulty, resp. slower, in the chromatogram.

As we did not observe, according to the above data, any considerable difference between the 2,4-D concentrations applied, we have continued carrying out the experiments with small doses, beginning the investigation of derivatives from the moment of their formation, resp. from the first day of treatment. For induction, in this case, we only used the indolic buffer, leaving infiltration out of consideration.

It may be established from the Table that the quantitative change in both indole-derivatives is uneven enough, here and there even sudden. From the first day after setting, the 6—OH—Indole could not be measured, either, resp. it did not give any spot. This is referring to that, even if it was originally contained — as verified by our previous investigation — in the water-plant, it must have been of minimum quantity, giving a measurable value only after being treated for some time with 2,4-D of a certain concentration. On the second day, 6—OH—Indole and 5—OH—Indole could already been demonstrated but only if treated with 3 and 6 ppm doses. After being treated in a 0.6 ppm concentration or in a control, however, there could not been demonstrated any. The fluctuating character of change could most be observed on the fourth day, when the quantity of both derivatives achieved in all the three concentrations a maximum value, although the 0.6 ppm-value couldn't even be measured by the same interval before that. After the fourth day, in any case, a strong decrease, but at the end of the treatment a little increase, were to be observed.

We wanted to check the species-specificity observed at measuring the peroxidase-enzyme activity in case of this method, as well. Therefore, the experimental series was performed, under similar conditions, in *Myriophyllum* sp., too, with the difference that, because of the maximum on the fourth day, the subsequent intervals were concentrated, in order to ensure a registration as exact as possible.

We see the appearance of species-specificity, on the one hand, in that a new derivate, not-observed as yet, manifests itself: 7—OH—Indole; on the other hand, that the quantity of both induced indole-derivates (5—OH—Indole, 7—OH—Indole) can only be measured in certain phases of experiments. In case of 5—OH—Indole,

Table 2. Change in indole derivatives in *Elodea canadensis*, as a result of a herbicide treatment in indolic buffer.

Indole derivative	Period of treatment (day)	2,4-D cc. (ppm)							
		0	0,6	3,0	6,0	0	0,6	3,0	6,0
		R _r -value				γ-quantity			
6—OH—indole	1	—	—	—	—	—	—	—	—
	2	—	—	0,22	0,23	—	—	10,0	4,5
	4	0,23	0,20	0,23	0,20	5,0	18,0	18,0	30,0
	8	0,17	0,17	0,17	0,17	1,3	1,7	1,7	2,3
	15	0,27	0,26	0,25	0,25	2,3	3,3	2,1	2,4
5—OH—indole	1	—	—	—	—	—	—	—	—
	2	—	—	0,29	0,32	—	—	4,5	3,8
	4	0,32	0,28	0,30	0,28	4,8	18,0	30,0	5,0
	8	0,25	0,25	0,25	0,25	1,4	1,8	2,4	1,7
	15	0,38	0,36	0,37	0,38	2,3	1,9	2,7	2,0

Table 3. Change in indole derivatives in *Myriophyllum* sp., as a result of a herbicide treatment in indolic buffer.

Indole derivative	Period of treatment (day)	2,4-D cc. (ppm)							
		0	0,6	3,0	6,0	0	0,6	3,0	6,0
		R _r -value				γ-quantity			
6—OH—indole	4	0,22	0,19	0,25	0,24	32,0	16,0	20,0	26,0
	5	0,21	0,22	0,21	0,19	4,0	14,0	5,0	5,0
	6	0,20	0,29	0,16	0,19	14,0	10,0	3,5	5,0
	8	0,17	0,18	0,16	0,17	4,5	5,0	18,0	5,0
	12	0,20	0,21	0,21	0,21	2,0	3,0	2,2	2,7
	15	0,20	0,19	0,16	0,20	4,2	4,5	3,7	4,0
5—OH—indole	4	0,28	0,27	0,32	0,32	20,0	10,0	16,0	16,0
	5	0,31	0,31	0,31	0,27	5,0	2,8	5,0	4,2
	6	0,27	0,39	0,29	0,30	3,7	3,8	3,3	3,8
	8	0,31	0,32	0,29	0,32	2,0	2,7	3,5	3,3
7—OH—indole	4	—	—	0,53	0,54	—	—	4,8	4,3
	5	—	—	0,49	0,51	—	—	16,0	4,8

on the 8th day we still got a spot in the chromatogram, at the next experimental point of time, on the 12th day, however, we got it no more. In case of 7—OH—Indole, the same took place on the 5th, resp. 6th day.

It can be established from our indole-hydroxylation measuring-series that the indole inductivity for the formation of new derivatives is not primarily given by the experimental medium, *e. g.* indolic buffer or infiltrated indole, but in a considerable part the 2,4-D of auxin-effect, and even species-specific factors, may have a role in it.

By the 2,4-D treatment, according to ARTEMENKO *et al.* (1971), the IAA-content is decreased, the IAA-oxidase level, and owing to this, the IAA-decarboxylation is increased. This is somewhat contrary to SÜDI's statements (1964), quoted above, and is throwing also a broader light upon the different ways of the synthesis of the aromatic compounds. In one of these reaction ways, from shikimi acid — through indole and some other intermediaries — tryptophan, and from this — in three possible ways — IAA are induced. The question arises if this synthesis is true the other way round as well, *i. e.*, whether IAA-degrading (mainly owing to the IAA oxidase) takes place in the same way. If it does, in the above sense, the decrease in IAA-content induced by the 2,4-D treatment must also influence the increase in the quantity of indole and its derivatives. Our experiment seems to verify this latter supposition: it is visible from Tables I and II that in case of every indole-derivative the value of control is lower than that of the treated ones but only up to the 8th day. On the 15th day, they already take an intermediate place. On the basis of all these, we may draw the conclusion that in water-plants — species-specifically — there exists the „reversed“ reaction way, as well (KERESZTES—HORVÁTH, 1977).

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COMPARISON OF METHODS FOR DETECTION OXYGEN UPTAKE IN YEASTS: THE AUTOMATIC COULOMETER AND THE WARBURG APPARATUS

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The oxygen uptake of four different yeast species has been determined by using an automatic coulometer as well as Warburg's method. While the two methods give nearly the same rate of oxygen consumption, small changes can be followed only when coulometric measurements are employed. The resulting oxygen uptake curves were fitted with a polynomial of third degree. Automatic coulometer has been found to provide not only extremely accurate but also convenient tool in determining oxygen uptake. The method seems to be generally applicable to the study of gas uptake of different biological and chemical systems.

Introduction

Oxygen uptake of biological systems is determined generally by manometric methods, in most cases using Warburg apparatus. When studying certain fine processes, particularly when the oxygen consumption in a reaction is to be unrevealed, however, the Warburg method is not sensitive enough.

In order to overcome the experimental difficulties DOBOS and GAÁL (1974) constructed an automatic coulometer which conveniently and precisely measures the uptake of small amount of gases. It is an especially useful tool when one is interested in the mechanism of simultaneous oxygen and hydrogen uptake. The consumed gases are supplied by electrolysis therefore the amount of reacted gases can be estimated from the coulombs needed to maintain the equilibrium states. As the measurement is reduced to a simple measurement of time, the method is easy to automatize.

In the present paper a comparison of the utility of the two methods is given. The applicability of the Warburg as well as the automatic coulometer methods are established in yeast model system.

Materials and Methods

The following yeast strains have been used: *Saccharomyces cerevisiae* RXII., *Candida utilis*, *Candida utilis* major, *Saccharomyces cerevisiae* EB4.

The yeasts have been cultured for 24 hours at 25 °C with continuous shaking. The culturing medium contained 5 g oxoid (Difco) and 10 g glucose dissolved in 1000 ml water.

The dry weights have been determined on an analytical balance after keeping the product at 110 °C in a desiccator filled with P_2O_5 for 2 hours.

Detection of mitochondria:

Nitro-BT dye has been used which reacts with the succinate-dehydrogenase in mitochondria. The product forms a blue colored complex. The cells have been incubated at 37 °C for 15 minutes in the following medium:

Sodium succinate	0,06 molar	1,0 ml
Nitro-BT dye	0,2 molar	2,5 ml
Phosphate buffer	0,2 molar	1,0 ml
KCl	0,6 molar	0,5 ml

Results and Discussion

The generally used technics have been applied to the determination of oxygen uptake in the Warburg apparatus. The wet weight of our initial sample was 0.01 g. Temperature was kept at 30 °C. Coulometric measurements were carried out under the same circumstances. Table 1. summarizes the oxygen uptake of the four yeast strains.

It is apperent from Table 1 that Sacch. cer. EB4 does not consume oxygen at all according to the coulometric method. The value obtained in the Warburg apparatus lies within the experimental error.

Table 1. Oxygen uptake of the studied yeast strains as measured in a Warburg apparatus and in a coulometer, respectively.

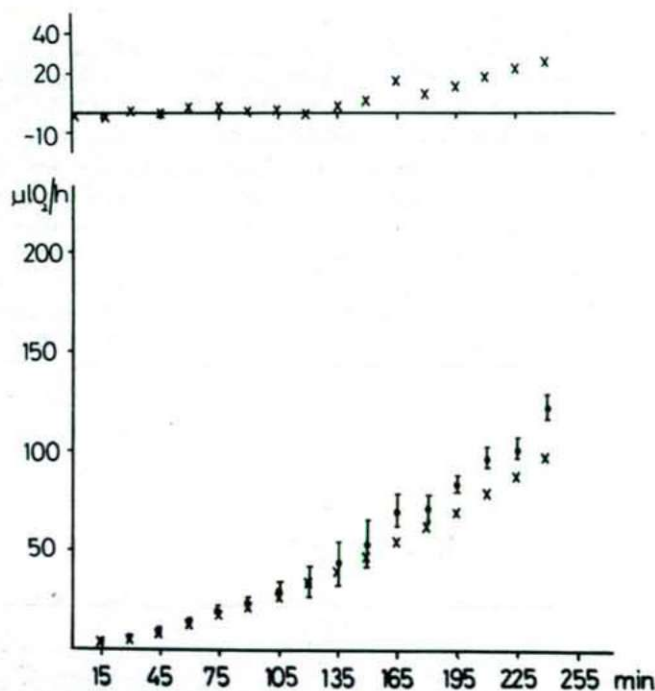


Fig. 1. Oxygen uptake of the Sacch. cer. RXII. strain in time obtained on the Warburg apparatus.

Table 1

Strain	Oxygen uptake microliter/mg dry weight hour	
	Warburg apparatus	Coulometer
Sacch. cer. RXII	101	135
Candida utilis major	85	97
Candida utilis	221	205
Sacch. cer. EB4	1,97	0,00

Sacch. cer. RXII has been selected for a comparison of the two methods in a time dependent oxygen uptake study.

Figure 1 shows the results collected on the Warburg apparatus. The experimental points are labeled with rings while the points of the corresponding third degrees polynomial fit are denoted with x. The deviation of the experimental points is indicated by vertical rods. Each point represents an average of three measurements. It can be seen that the third degree polynomial fit describes the experimental pattern very well until the reaction time is short enough.

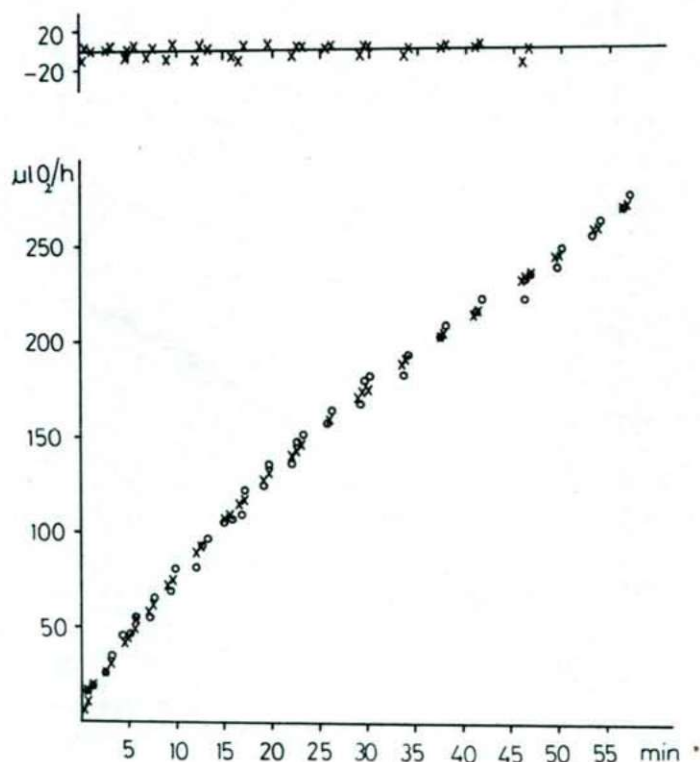


Fig. 2. The same as measured with the coulometric method.

The deviation of the two curves becomes pronounced only after a longer reaction time. The parameters of the polynom were computed using the least square method. Values in Figure 1 are not corrected for the cell number growth in time, therefore they differ from those given in Table 1.

The third degree polynom is given as where b_0 , b_1 , b_2 , and b_3 , are the respective regression coefficients.

In Figure 2 the oxygen uptake of the same yeast culture is plotted as measured by the coulometric method. Denotations are the same as in Figure 1.

A comparison of the two figures reveals that the coulometric method is more accurate and as a result the points are better fitted with the third degree polynom. In contrast to the curve obtained with the Warburg apparatus, here the computed values does not differ from the experimental ones even at long reaction times.

We have found in previous studies that ethidium bromide inhibits oxygen uptake. The mechanism of this phenomenon was investigated with the more exact coulometric method.

Administering ethidium bromide at the start of the experiment will produce a stable state by the 15th minute which remains unchanged during the next 24 hours. The observation is in line with the hypothesis that the principal effect of ethidium

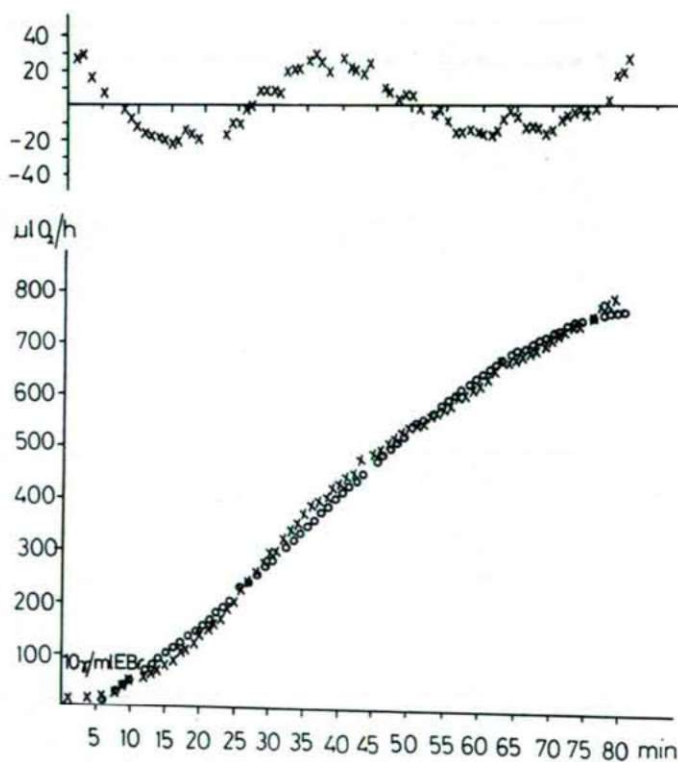


Fig. 3. Coulometric study on ethidium bromide inhibition of oxygen uptake in time. EBr concentration 10^{-5} g/ml.

bromide is degradation of mitochondrial DNA. Since several important enzymes of respiration are partly or wholly coded in mitochondrial DNA ethidium bromide does affect respiration but only following a delay phase. This is the time needed for the decomposition of the enzymes as well as the DNA. In two days respiration deficient mutants can be isolated displaying no respiratory activity.

One can see in Figure 3 that adding ethidium bromide in the 5 th minute of the experiment decreases reaction rate during the next 15 minutes then oxygen uptake returns to close to normal. Such small change is not detectable in the Warburg apparatus.

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ANATOMY OF THE NERVOUS SYSTEM OF MAYFLY LARVAE (PALINGENIA LONGICAUDA OLIV)

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Abstract

The nervous system of the mayfly larva is a modified ventral nervous cord, the ancient traits of which are the double connectives providing segmentation and the partial fusion inside segments. Its characteristic, pointing to the development, is the formation of complexes of the third thoracic and seventh abdominal ganglia. Comparison of the results with other literature data indicates that the mayfly is one of the most ancient species of the Ephemeroptera.

Introduction

In recent years, research into the life, organizational construction, and occurrence of the Arthropoda has become more and more comprehensive. It is understandable therefore, that such knowledge relating to the Ephemeroptera is being completed with an ever increasing number of data.

The mayflies, that representing one of the most ancient groups of the present-day Arthropoda, may afford a reliable starting-point for the solution of a number of problematical questions (mainly with respect to evolution, but often morphology or anatomy, as well).

The peculiar, hidden life, long development, and restricted geographical occurrence of the mayfly (*Palingenia longicauda*) larva are all factors explaining why we know comparatively little about the constructions of their organisms and organs (LANDA, 1969; SWAMMERDAM, 1675).

In the present paper, our aim was an exact anatomical study of the central nervous system of the larva. This work will serve as the basis for further of our results a waiting publication.

Materials and Methods

The larvae used in our investigations were collected from the rivers Tisza and Maros. Studies were carried out on larvae in different stages of development, but our findings and photographs all refer to the larvae in the last year of their life. (It is to be noted that the localization of the ganglia and the course of the nerves are similar in the younger larvae the only differences observed related to their sizes.)

The larvae collected were fixed partly in 70 per cent alcohol, and partly in 10 per cent neutral formalin. To facilitate study of the localization of the ganglia and the courses of the nerves, STEINMANN'S (1960a) negative staining technique was applied.

Results and discussion

The nervous system of the larva is a double ventral nerve cord. It has preserved the ancient features (double connectives, segmentation) in many respects, but, at the same time, in the case of the ganglia of the nerve cord, we could observe further fusions.

Similarly to other Arthropoda, three main parts may be distinguished in its nervous system: the oesophageal nerve ring, the thoracic and the abdominal ganglia (DUPORTE, 1915; HANSTRÖM, 1928; PETERSON, 1912; WEBER, 1966).

The cerebral ganglia forming the oesophageal nerve ring (ggl. supraoesopha-

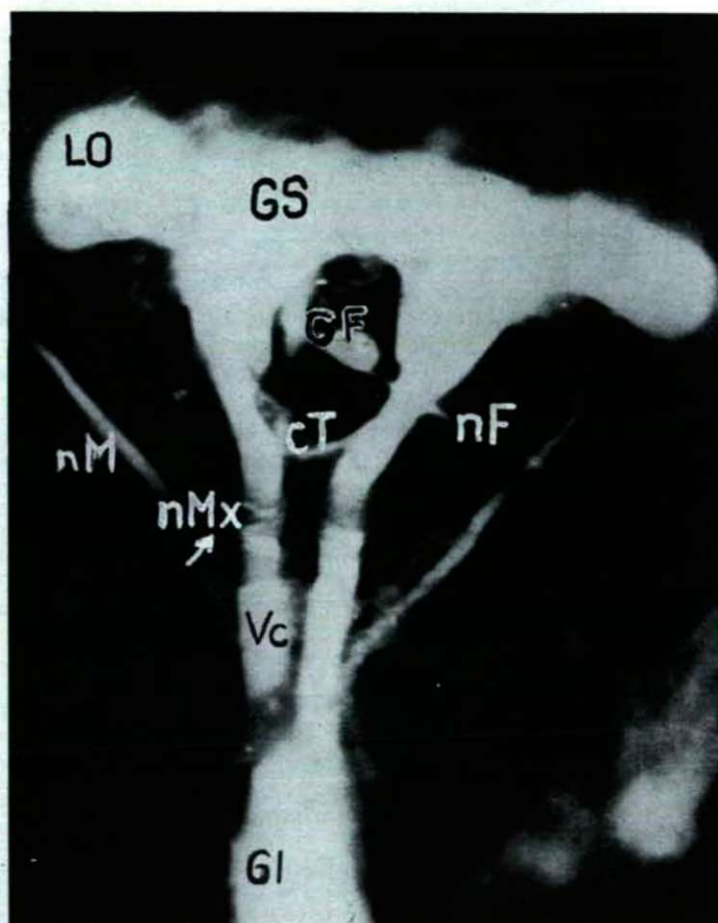


Plate 1. Oesophageal nerve ring of the *Palingenia longicauda* larva ($\times 45$).

(CT=commissura tritocerebralis, GF=ganglion frontale, GI=ganglion infraoesophageum, GS=ganglion supraoesophageum, LO=lobus opticus, nF=nervus frontalis, nM=nervus mandibularis, nMx=nervus maxillaris, Vc=connectivum ventrale).

geum), the suboesophageal ganglion (ggl. infraoesophageum), and the connectives between them can be well differentiated (Plate 1).

The cerebral ganglion (with the largest dimensions) has grown together out of three paired ganglia, and consequently it can be divided into three cerebral sections (HANSTRÖM, 1928; PETERSON, 1912; STEINMANN, 1966b; WEBER, 1966). Its anterior part is the protocerebrum, divided into two parts by the intercerebral fossa. At its lateral part the lobus opticus (of similarly large extent) appears with the strongly pigmented eyes. Somewhat laterally from the intercerebral fossa, symmetrically, the nerves of the point (simple) eyes may be observed.

The deutocerebrum, occupying the central site, grows more narrow as it proceeds backwards. The sensory and motor fibres of the nerves of the antenna, as well as the frontal nerves, are localized dorso-laterally. The former leave the brain in a common nerve, but the sensory and motor fibres soon branch off.

The tritocerebrum turns backwards in the ventral direction, grows quite narrow, and runs close to the pharynx. Its biggest nerve, the upper nervus labralis, starts out of the ventral side of the brain. On the medial side of the third brain section the only cerebral commissure, the tritocerebral commissure, is to be seen. In the beginning, the first ventral connective runs parallel with this, joining the brain to the suboesophageal ganglion (ggl. infraoesophageum). The nerves leaving the suboesophageal ganglion are vigorous. These are the nervus mandibularis, the nervus maxillaris and the nervus labialis. In the mayfly larvae (just as in the chewing insects) these nerves are powerfully developed (KÜKENTHAL et al., 1930; STEINMANN, 1960b; 1962; VAJON, 1970; WEBER, 1966).

From a comparison of the nervous systems of the larvae and imagos it was possible to establish that these nerves were poorly developed in the imagos, and progressively degenerated in time before development into the imago.

The ggl. frontale is to be found in the oesophageal nerve ring. It is joined to the tritocerebrum by a very thin small nerve. Starting from the ganglion, the nerve runs backwards at the dorsal part of the alimentary canal.

The suboesophageal ganglion is joined by ventral connective II to thoracic ganglion I (Plate 2). In the area of the thorax three dorso-ventrally flattened paired ganglia can be found, corresponding to the three thoracic segments. The ganglia are joined together by paired connectives. A big nerve, the nervus ventralis, emerges laterally from every ganglion. This soon divides into several branches, bringing about a plexus (Plate 3, Fig. 2). The branches innervate the longitudinal muscles of the ventral side.

The nerves (nervus lateralis) originating in the anterior-lateral part of the ganglia innervate the dorsal longitudinal muscles and those lying orbicularly in the segments (CAMPBELL, 1961; EWER, 1954; GREGORY, 1974). An unpaired nerve, the nervus medialis, originates from the ventral side of the ganglia. For a while this runs parallel with the longitudinal connectives linking the two ganglia. It then divides into two branches, the transversal nerves. The nervus medialis and nervus transversalis are also parts of the sympathetic nervous system (PETERSON, 1912, SRIVASTAVA, 1972; VAJON, 1962). In thoracic ganglion III, there originate other nerves, apart from those mentioned above, from the posterior-lateral part of the ganglion (Plate 2, Plate 3, Fig. 1). These go over from the third thoracic segment into the first abdominal segment. There they divide into two branches, innervating the dorsal, and ventral

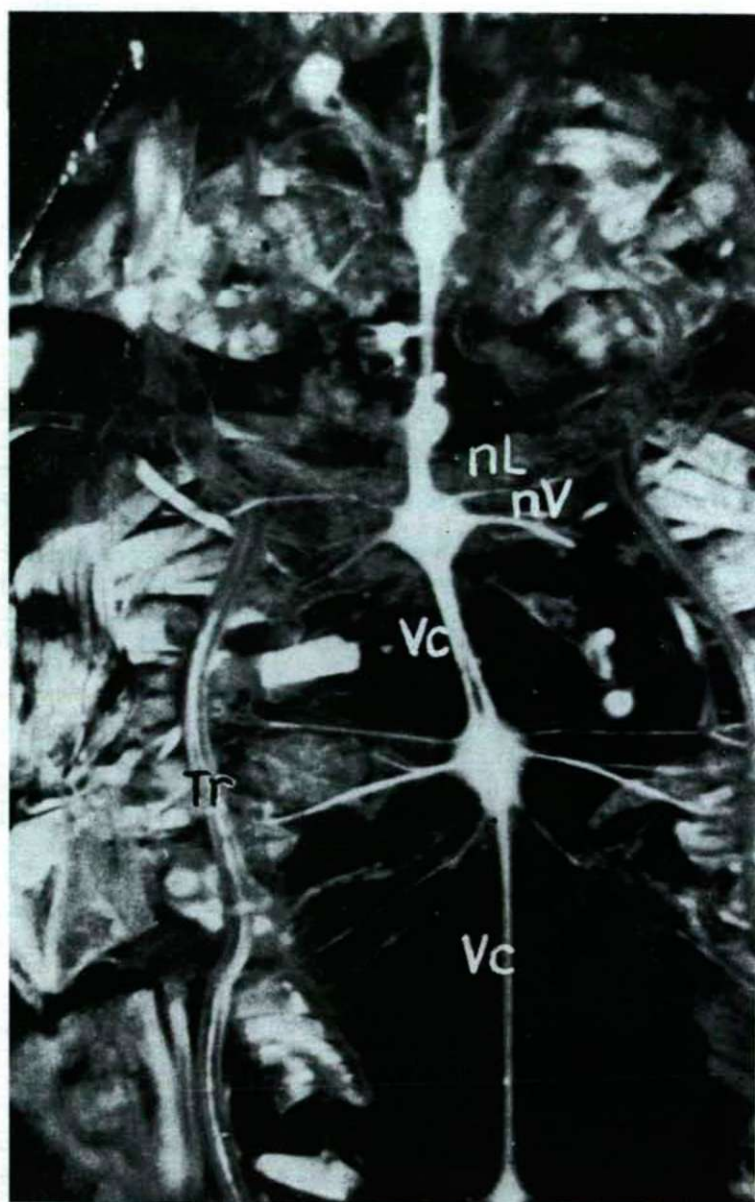


Plate 2. Thoracic ganglia of the larva ($\times 17$).

(nL=nervus lateralis, nV=nervus ventralis, Tr=trachea, Vc=connectivum ventrale).

muscles of the first abdominal segment (KÜKENTHAL et al., 1930). In the first abdominal segment no ganglion was found. We assume that in the course of the embryonal development this ganglion fused with the last thoracic ganglion (ggl. metathoracale).

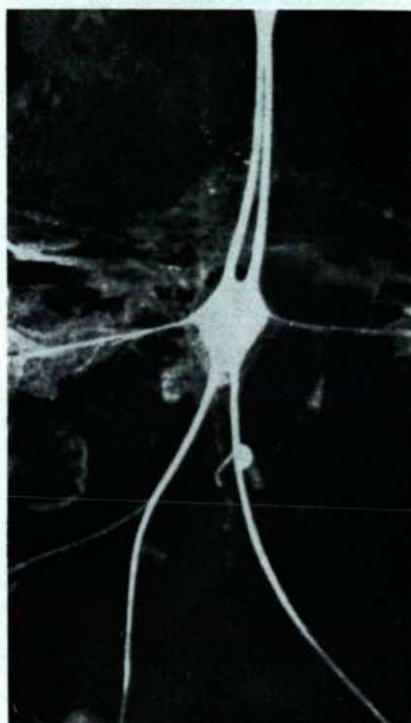
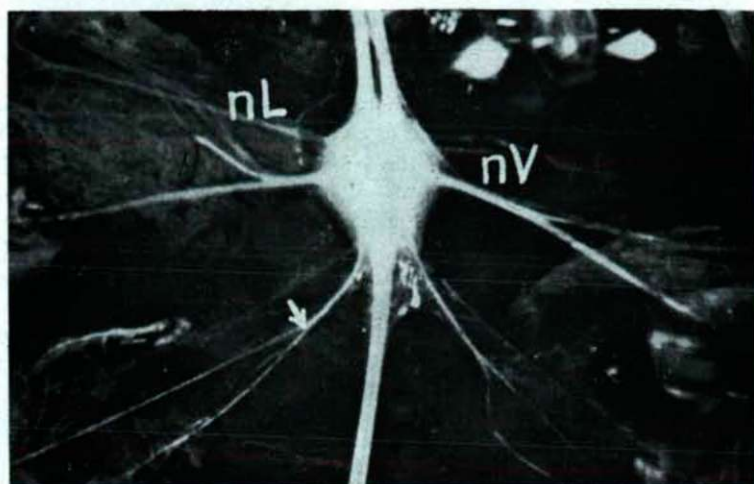


Plate 3. Fig. 1. Magnified picture of the third thoracic ganglion ($\times 24$). (nL=nervus lateralis, nV=nervus ventralis. The arrow indicates the nerves going over to the first abdominal segment).
 Fig. 2. A detail of the thoracic ganglia ($\times 25$). (The arrow indicates the plexus system of the nervus ventralis).
 Fig. 3. Ganglion abdominale VII ($\times 30$).

This seems to be verified by the extreme length of the connective lying between the third thoracic and the effectively first abdominal ganglia (in abdominal segment 2), being about twice as long as the others.

In the eleven segments of the abdomen seven abdominal ganglia can be found, lying in segments 2 to 9. The last of the seven ganglia (ggl. abdominale VII) is a ganglionic complex brought about by the fusion of three paired ganglia (BIRKET—SMITH, 1971). Ggl. abdominale VII (Plate 3, Fig. 3) ends in two powerful nerves, bringing about with their further branches the somatic nerves of the last abdominal segments.

Comparison of the nervous systems of the larva and imago revealed the considerable identity in the positions of the ganglia.

It can be said of the Arthropoda in general, including the mayfly, that the degree of development of the central nervous system is determined by the extent to which it is concentrated. This concentration is of low degree in the species studied, because it can be observed only at the third thoracic and seventh abdominal ganglia. Hence, ten paired ganglia may be found in the body of the mayfly. This confirms that the mayfly may be considered one of the most ancient Ephemeroptera species (KÜKEN—THAL et al., 1930; LANDA, 1969). The degree of brain development, of course, must not be left out of consideration, either. However in our opinion, the latter may be characterized within the Arthropoda not so much by changes in dimension as by structural changes.

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FOOD-BIOLOGICAL INVESTIGATIONS ON THE FOX POPULATIONS IN SOUTHERN HUNGARY

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Abstract

In 501 sq.km (between March 1974 and December 1975) 133 fox gastric content, 433 animal remains, and 499 prey remains and excrements were investigated. The percentage of damage and use depends upon the season, the territorial features, and the amount of prey and foxes. The fox is noxious in an intensive small-game area where its tolerable density is 0,14—0,10 fox/sq.km. On the other hand, it is useful in an agricultural district when the noxious rodents became too numerous. Otherwise it is indifferent but its population density should not outnumber 0,17—0,20 fox/sq.km because, as a result of its fecundity, it is difficult to maintain its number.

Introduction

It is a common distinctive feature of the defective data of Hungarian literature that the fox is not investigated as a member of the biocenosis, but that anthropocentric polemics are pursued about its economic damage and utility. Lacking methodical food-biological investigations, some authors try on the basis of a few observations or cases to qualify the fox as expressly useful, and other Hungarian authors as expressly noxious or as indifferent.

Foreign researchers are also interested in the problems of use and damage induced by the fox, but in addition, the fox-research there is also motivated by other factors. There are many more foxes elsewhere than in Hungary and that may produce every now and then great rabietic epidemics. SPITTLER (1972) established in Nordrhein-Westfalen that the decrease in the number of foxes was always followed by an increase in the stock of useful small game. The connections between the stock-increase in hares and partridges, with respect to the decrease in the stock of foxes can be demonstrated and expressed even in percentage of the basis of hunting spoils. The different kinds of food are classified by SPITTLER (1972), by reason of their character, into five groups: (1) meat, (2) mice, (3) insects, (4) plants, (5) that of other origin. According to KOENAN (1952), the everyday food of the fox is the mouse. According to PETZSCH (1966), the fox yields a not negligible profit, but weighing the pros and cons of use and damage together, it may nonetheless be considered as noxious. According to BEHRENDT (1955), meat is the principle component of the total food. ENGLUND established (1965) that the composition of gastric contents changed continually and dynamically according to the location, season, period, the number of some kinds of prey and foxes, weather, geographical, and other factors. In the prey-list drawn up by him the noxious rodents occurred most frequently among the mammals. Foxes

seem to prefer voles to mice. LOCKIE (1957), Scott and KLIMSTRA (1955) also agree with this, although the number of mice is generally higher. According to LUND (1967), the fox expressly picks and chooses among the small rodents, preferring voles to mice.

In the research material of PAVLOV, LARIN, and GRIBOV (1961) most remains are derived from small rodents. These are followed in order by birds. According to GUZDEV, SOLDATOVA, and BOCHAROVA (1957) mostly rodents, among them field-voles, are hunted by the fox. According to PAVLOV and KIRIS (1956), fish, reptile and amphibian are consumed by the fox but as a last resort. Carrion-eating is a common phenomenon in the fox, although it is not always possible to establish (e. g., with poultry) if in the case investigated it was a dead or a stolen specimen, (ENGLUND, 1965). According to MCINTOSH (1963) in the district Canberra in winter, the most important food of foxes is dead sheep. According to MARTENS' information (1971), emu and kangaroo carcasses are also consumed by foxes willingly.

Materials and Methods

In order to establish, what the extent of damage and use induced by foxes in Southern Hungary is, and what the tolerable population level is, I have carried out investigations. The area of investigation was 50,100 ha, consisting of three zones (cf. the sketch map). Zone "A" was 7,600 ha, zone "B" 37,000 ha, and zone "C" 5,600 ha. The height above mean sea level was 78—85 m above the Adriatic. The relief is a perfect plain. In the area mentioned — between March 1974 and December 1975 — the gastric content of 133 foxes, 433 piece animal remains, and 499 prey-remains and excrements found on the ground were investigated. The detailed aims and points of view of my investigations were the following:

1. To analyse the frequency of the single kinds of prey, on the basis of the remains found in the stomach.
2. To establish the relative content of the stomachs investigated.
3. To calculate the total gastric content (biomass).
4. To find the frequency of the occurrence of the single kinds of prey, as compared to the number of stomachs.
5. To make a species-list of prey-animals, on the basis of the gastric contents.
6. To analyse the frequency of the single kinds of prey, on the basis of the remains and excrements found on the ground.
7. To make a list of prey-animals, on the basis of the remains and excrements found on the ground.

Results

1. The single kinds of prey occur in the menu of the fox with different frequencies. The most frequent prey was mammals, which were consumed 52,7 per cent of the time (Cf.: Table 1). The game birds were carried away by the fox mainly in the period of hatching and raising the little chickens. In case of pheasants, even the sex could usually be established, because of the feather-remains from the breast and neck area. In Autumn and Winter, the prey was nearly always a cock, and in Spring and Summer a hen. Small, noxious rodents are also an important food for the fox. Among these, the frequency of the different voles is the highest but it changes according to the seasons. Insects occurred in Summer, with a surprisingly high frequency, but this didn't mean a large proportion of the total food. In the different zones, the single kinds of prey did not occur with the same frequency (cf. Table 1).

2. The summary of the relative gastric contents according to zones shows that the frequency of the single kinds of prey is not always correlated with the relative content, in the zones. This follows from the different sizes of the single animal species, as well. Although the brown hare occurred, e.g., in zone "A" only with a 5,5 per cent frequency, and in zone "B" with a 3,5 per cent frequency, it took part in the relative gastric contents in zone "A" 22,4 per cent of the time, and in zone "B" 18,3 per cent of the time. The small, noxious rodents are closely correlated with one another. The most mispropotioned conditions are observed with insects and plants (cf. Table 1 and Fig. 1).

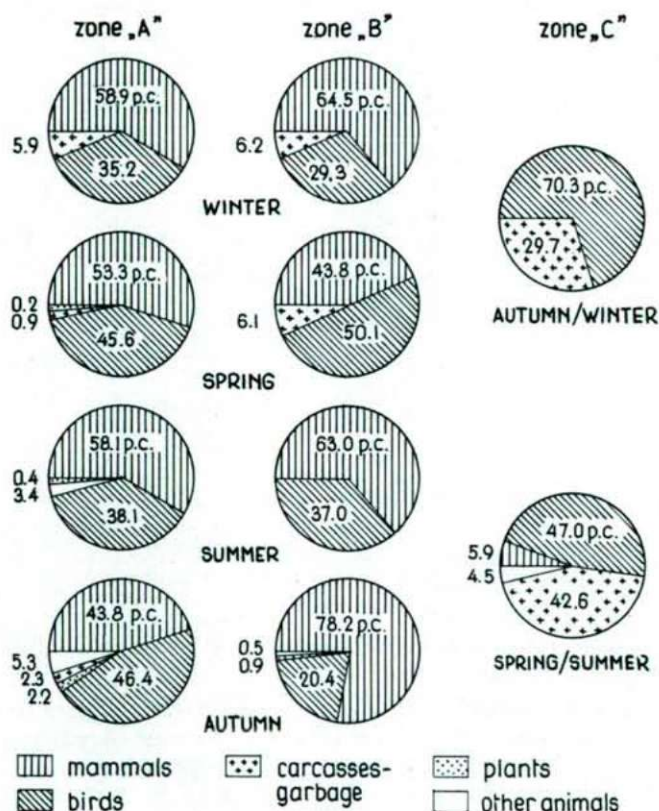


Fig. 1. Relative gastric content.

3. After summarizing all the gastric contents in the area investigated during the period of investigation (1974—1975), the total gastric content was 19,916.4 g. There fell to one stomach an average of 149,7 g. Breaking down the row to 50 g-parts from 5 to 351 g, most stomachs (29) contained between the weight limits of 29 to 200 g. Taking into account the empty stomachs, 66 stomachs contained less than 151 g. With respect to the average weight of gastric contents, there is no essential difference between and within zones, between seasons, and between sexes. But in the stomach

Table 1. Analysis of the frequency of some kinds of prey on the basis of gastric contents (1974—1975).

		201		203		29		433	
		p i e c e s							
Total prey		“A”		“B”		“C”		together	
		z o n e s							
		number p.c.		number p.c.		number p.c.		number p.c.	
A)	Plants	6	3.0	3	1.5	1	3.5	10	2.3
B)	Invertebrata	48	23.9	55	27.1	—	—	103	23.8
	Mollusca	2	1.0	—	—	—	—	2	0.4
	Insects	46	22.9	55	27.1	—	—	101	23.4
C)	Vertebrata	143	71.1	143	70.4	18	62.0	304	70.2
	Fish	—	—	—	—	1	3.5	1	0.2
	Amphibia	3	1.5	—	—	—	—	3	0.7
	Reptilia	—	—	—	—	1	3.4	1	0.2
	Birds	31	15.4	29	14.3	11	37.9	71	16.4
	game birds	17	8.4	11	5.4	—	—	28	6.5
	poultry	1	0.5	1	0.5	4	13.8	6	1.4
	other birds (and eggs)	13	6.5	17	8.4	7	24.1	37	8.5
	Mammals	109	54.2	114	56.1	5	17.2	228	52.7
	Insectivores	6	3.0	2	1.0	3	10.3	11	2.5
	brown hare	11	5.5	7	3.5	—	—	18	4.2
	mice	16	8.0	37	18.1	2	6.9	55	12.7
	voles	73	36.2	52	25.6	—	—	125	28.9
	hamster/gopher	3	1.5	16	7.9	—	—	19	4.4
D)	Carcasses and								
	garbage	4	2.0	2	1.0	10	34.5	16	3.7
	carcasses	4	2.0	2	1.0	1	3.5	7	1.6
	garbage	—	—	—	—	9	31.0	9	2.1

of young foxes much less food could be found, and even that was of mixed composition, often only carcasses and garbage.

4. I have mostly observed mammals, birds, carcasses and garbage in stomachs. In zone "A" 20 stomachs only contained mammals, out of which 11 were small rodents, and nine brown hares. But brown hares were only found in 11 stomachs and small rodents in 21. An explanation is that the fox, after being satiated with hare, does not feel the need to take further food. The same may also be observed after the consumption of pheasant. In spite of this, in the overwhelming majority of cases, the stomachs exposed did not contain any useful game (cf. Table 2 and Fig. 3).

5. In the gastric contents, I have determined the following species. The numbers after species-names denote the number of pieces of remains.

a) Plants

<i>Rubus caesius</i>	5
undetermined species	5

b) Invertebrata

Gastropoda — not determined in detail	2
Insecta	
Acridoidea — not determined in detail	32
Tettigonioideae — not determined in detail	31
Coleoptera	
<i>Geotrupes mutator</i>	7
<i>Anoxia orientalis</i>	5
<i>Polyphylla fullo</i>	3

c) Vertebrata

Pisces	
<i>Carassius auratus gibelio</i>	1
Amphibia	
Anura — not determined in detail	3
Reptilia	
<i>Lacerta agilis</i>	1
Aves	
<i>Phasianus colchicus</i>	23
<i>Perdix perdix</i>	2
<i>Anas platyrhynchos</i>	2
<i>A. crecca</i>	1
<i>Gallus domestica</i>	5
<i>Corvus frugilegus</i>	1
<i>C. cornix</i>	1
<i>Garrulus glandarius</i>	1
<i>Pica pica</i>	1
<i>Columba domestica</i>	1
<i>Streptopelia decaocto</i>	3
<i>S. turtur</i>	1
<i>Galerida cristata</i>	1
<i>Sturnus vulgaris</i>	1
<i>Turdus pilaris</i>	1
<i>Passer montanus</i>	4
<i>Carduelis carduelis</i>	1
<i>Parus major</i>	1
<i>Vanellus vanellus</i>	1
<i>Larus ridibundus</i>	1
<i>Fulica atra</i>	2
undetermined species	2
eggs	15

Mammalia

<i>Lepus europaeus</i>	18
<i>Apodemus sylvaticus</i> and <i>Mus spicilegus</i>	44
<i>A. agrarius</i>	4

<i>Micromys minutus</i>	5
<i>Rattus norvegicus</i>	2
<i>Clethrionomys glareolus</i>	48
<i>Microtus arvalis</i>	57
<i>Pitymus subterraneus</i>	16
<i>Arvicola terrestris</i>	3
<i>Ondathra zibethicus</i>	1
<i>Cricetus cricetus</i>	13
<i>Citellus citellus</i>	6
<i>Erinaceus europaeus</i>	1
<i>Talpa europaea</i>	1
<i>Sorex araneus</i>	6
<i>Neomys fodiens</i>	3

d) Carcasses and garbage

Carcasses	
<i>Capreolus capreolus</i>	1
<i>Anser erythropus</i>	1
<i>A. domestica</i>	1
<i>Meleagris gallopavo</i>	1
undetermined species	3
Garbage	
pork-lard	1
sausage	1
pork	1
bread	1
potatoes	1
paper	2
hide	1
plastic	2

6. In the stomach only food-remains referring to a certain point of time can be found. But in the neighbourhood of burrows food-remains referring to a longer period can be found, provided that these — owing to their quality — do remain for a longer, than a shorter time. Included in this class, for instance, are some bone remains, feathers, and various finds in excrements. The frequency of some species is many times greater than the frequency calculated from the gastric contents, e.g., that of the hamster (cf. Tables 1 and 3). That of birds is also higher. The reason for this is that the parts of some species, left over by the fox (e.g., the wing of the pheasant) do remain for a long time. The remains found in the burrows and their close neighbourhood cannot replace, even if systematized, the prey and species lists made on the basis of the stomachs exposed. They may call attention to certain facts (in the present case to the extreme frequency of hamsters) that otherwise would remain obscure. I omit publishing a species-list made on the basis of remains found on the ground because its data are already summarized in Table 3.

My investigations performed on the food-biology of the fox (*Vulpes vulpes* L.) on the basis of the animal-remains found in the stomachs and of prey-remains and

Table 2. Comparison of the number of pieces of prey to the number of the receiving stomachs (1974—1975).

Total number of stomachs		62		62		9		133	
		“A”		“B”		“C”		together	
		z o n e s							
		prey	stom.	prey	stom.	prey	stom.	prey	stom.
		p i e c e s							
A)	Plants	6	6	3	1	1	1	10	10
B)	Invertebrata	48	6	55	4	—	—	103	10
	Mollusca	2	2	—	—	—	—	2	2
	Insects	46	4	55	4	—	—	101	8
C)	Vertebrata	143	—	143	—	18	—	304	—
	Fish	—	—	—	—	1	1	1	1
	Amphibia	3	1	—	—	—	—	3	1
	Reptilia	—	—	—	—	1	1	1	1
	Birds	31	28	29	25	11	6	71	59
	game birds	17	17	11	11	—	—	28	28
	poultry	1	1	1	1	4	4	6	6
	other birds (and eggs)	13	10	17	13	7	2	37	25
	Mammals	109	33	114	39	5	2	228	74
	insectivores	6	1	2	2	3	1	11	4
	brown hare	11	11	7	7	—	—	18	18
	mice	16	6	37	7	2	1	55	14
	voles	73	13	52	11	—	—	125	24
	hamster/gopher	3	2	16	12	—	—	19	14
D)	Carcasses and								
	garbage	4	4	2	2	10	6	16	12
	carcasses	4	4	2	2	1	1	7	7
	garbage	—	—	—	—	9	5	9	5

excrements, are summarized in the following. The data on the population-density are determined on the basis of number-estimation (applying statistics of shooting and visual observations).

The relative ratio and frequency of some kinds of prey change in the gastric contents. The ratio of use and damage also changes. It depends on the season and zone (cf. Figs. 1 and 2).

In the stomachs, both with respect to the total weight and to the relative content, mammals, birds, carcasses and garbage constitute most of the prey. Mammals and birds are vertebrata. Invertebrata, and plants contributed minimally to the gastric contents analyzed.

In the fox population living in the neighbourhood of gargabe-heaps containing digestible organic matter no individuals with an empty stomach were found during the investigation.

Rodents accruing frequently in the area investigated also occur more frequently in the prey. Rodents found rather rarely are also rare in the prey.

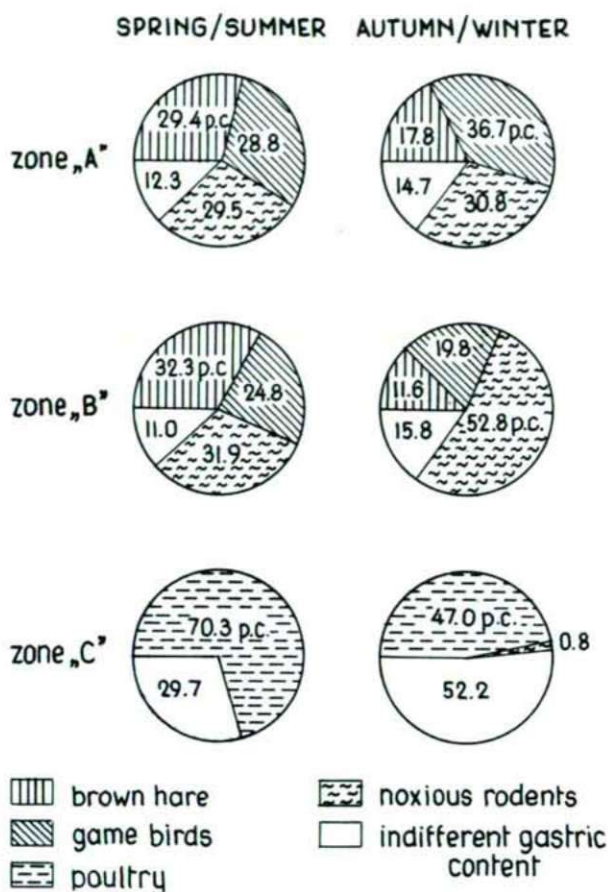


Fig. 2. Use and damage on the basis of the relative gastric content.

From the bird species living wild in the area investigated, only the pheasant can be found with high frequency in the prey-list. The other species, in however large numbers they live in the area, occur only occasionally in the prey-list.

In winter, the wounded cock-pheasant is prey more frequently than the hen-pheasant. In spring and summer, due to hatching, the pheasant is more frequent.

The massacre of brown hares and game birds, as well as the stealing of poultry, may be regarded as a harmful activity of the fox.

On the other hand, the destruction of the noxious rodents, and the cleansing role it carries out as a so-called „litter-bearer“ in forests and meadows are to its credit.

In the area investigated, the activity of the populations living in zone „A“ is expressly harmful owing to the destruction, mainly in spring and summer, of the nesting pheasants with their nestlings. But the activity of the populations living in

Table 3. Analysis of the frequency of some kinds of prey on the basis of remains and excrements found on the ground (1974—1975).

No. of finds		112		259		78		449	
		“A”		“B”		“C”		together	
		z o n e s							
		piece	p.c.	piece	p.c.	piece	p.c.	piece	p.c.
A)	Plants	5	4.5	2	0.7	—	—	7	1.6
B)	Invertebrata	23	20.5	8	3.1	2	2.6	33	7.3
	Mollusca	3	2.7	—	—	—	—	3	0.7
	Insects	20	17.8	8	3.1	2	2.6	30	6.6
C)	Vertebrata	82	73.2	249	96.2	53	67.9	384	85.5
	Fish	2	1.8	—	—	1	1.3	3	0.7
	Reptilia	1	0.9	—	—	—	—	1	0.2
	Birds	43	38.4	16	6.2	47	60.2	106	23.6
	game birds	27	24.1	9	3.5	4	5.1	40	8.9
	poultry	2	1.8	2	0.7	39	50.0	43	9.6
	other birds (and eggs)	14	12.5	5	2.0	4	5.1	23	5.1
	Mammals	36	32.1	233	90.0	5	6.4	274	61.0
	insectivores	3	2.7	—	—	—	—	3	0.7
	brown hare	7	6.2	8	3.1	4	5.1	19	4.2
	mice	9	8.0	9	3.5	1	1.3	19	4.2
	voles	14	12.5	13	5.0	—	—	27	6.0
	hamster/gopher	3	2.7	203	78.4	—	—	206	45.9
D)	Carcasses and								
	garbage	2	1.8	—	—	23	29.5	25	5.6
	carcasses	2	1.8	—	—	5	6.4	7	1.6
	garbage	—	—	—	—	18	23.1	18	4.0

zone "B" is expressly useful in spring and summer, owing to the destruction of the noxious rodents (cf. Fig. 2).

All their other activities are indifferent from the point of view of man.

The number of foxes living in the area investigated is somewhat above that tolerable. The 0,23 fox/sq.km density must be decreased to 0,17—0,20 fox/sq.km. This means that one fox may occur in 500—600 ha.

In the areas that, owing to their conditions, are particularly suitable for pheasant nesting, the locally tolerable number ought to be decreased to a 0,14—0,10 fox/sq.km density. This means that one fox may occur in 700—1.000 ha. So many foxes, however, are necessary, mainly for hygienic reasons.

The fox is at the end of the food-chain and, in the area, there is no longer any natural enemy that would impede its multiplication. This activity remains, therefore, the task of the man.

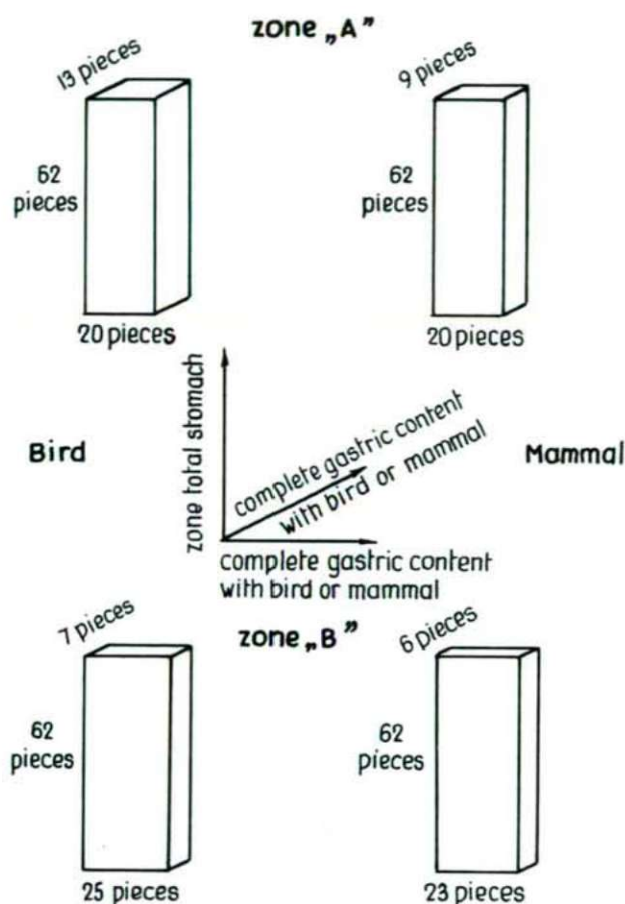


Fig. 3. Frequency of the complete gastric contents in case of birds and mammals.

As a procedure for reducing their number I don't propose poisoning (bait) and gassing. The food and eggs poisoned will damage the fox least. The protected and very rare birds of prey, however, often take them up. As for taking poisonous gas out into nature and into the hunting-ground, I refuse that on principle.

In order to impose restrictions on the number of foxes, I suggest the hunting-like procedures: shooting, foxdriving, and in the vicinity of breeding stations I propose trapping.

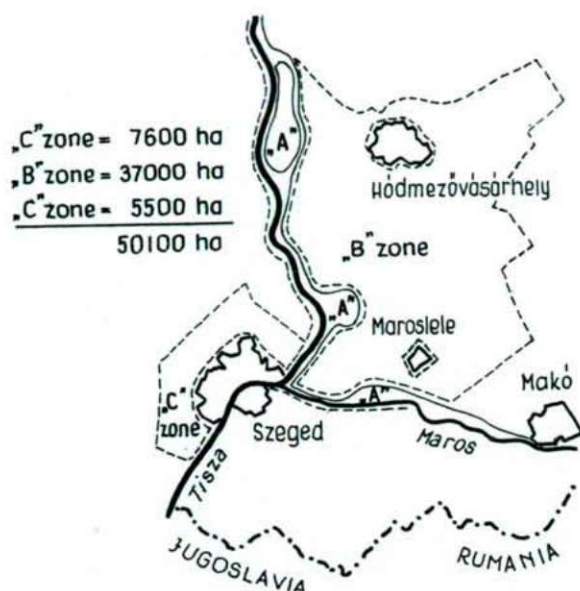


Fig. 4. Area of investigation (Sketch map).

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DATA ON THE VERTICAL DISTRIBUTION OF ZOOBENTHOS IN SALINE "LAKES" AND RIVERS

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Abstract

In the course of investigating the vertical distribution of the zoobenthos and comparing the cases of the small, astatic saline lakes to the river Tisza, we obtained the following results:

a) There could be observed a vertical distribution (with special respect for the maximum values and varying in the single collections), mainly in cases of Oligochaeta, Ephemeroptera, as well as Ceratopogonida and Chironomida.

b) In both water-types, about half of the zoobenthos lives in the upper 10 cm layer. The vertical distribution of the taxons occur equally in both watertypes (Chironomida, Ceratopogonida) is similar.

c) The change in the water-level and drying up governs the vertical distribution of zoobenthos. The groups Chironomida and Coleoptera are respond in a similar way. Chironomida and Ceratopogonida, however, respond oppositely.

Introduction

The qualitative and quantitative, space and time distribution of the zoobenthos of waters is influenced by abiotic and biotic factors. The knowledge of the structure, and the material-energy circulation of ecosystems is increased by revealing the causal relations of population dynamics.

It is only justified from special points of view to compare the zoobenthos of rivers and standing waters with each other. The vertical quantitative distribution and the horizontal quantitative distribution of the zoobenthos taxons in the sediment may be considered such.

The zoobenthos density — according to my investigations — diminishes in horizontal and vertical directions — from the river — and lakeside towards the middle of watercourse, and from the surface towards the deeper layers of the sediment in the river and standing waters of this country.

The life of sediment-dweller organisms at the bottom surface and their vertical movement are determined by several factors, of course, but the single populations react to these factors in different ways. In the course of my preliminary investigations I could establish mainly the vertical distribution and only the quantitative conditions of that. It is a task of further investigations, to reveal the causative relations.

Materials and Methods

In order to get reliable results from the investigation of the vertical distribution, the methods have to be improved to eliminate or at least minimize the loss of animals during sampling. It is a problem to separate the bottom samples into layers, and to stabilize in original situ the bottom fauna (EFFORD, 1960; COLEMAN—HYNES, 1970; BRINKHURST—BATOOSINGH, 1969; FERENCZ, 1968).

To remove the deposit, a 425 mm long cylindrical corer of 84 mm diameter was used (FERENCZ, 1968). The samples were cut into 5, or 10 cm parts in the field. Then in the laboratory, eluting them through a 0.28 mm mesh metal sieve, we selected the animals, fixed in 6 per cent formalin according to taxon-groups and evaluated them quantitatively. The Mollusca group was omitted, because those living there and the empty shells carried along by water are confusable, that is to say, the subfossil and recent ones are undistinguishable, and our results would have been unreal with respect to a vertical distribution of Molluscs.

Because of the sampling-technical conditions, the bottom samples of the saline waters were separated and examined in 5 cm, and those of the river Tisza in 10 cm layers. It is to be noted that we don't regard the investigation of bottom layers thicker than 5 cm, fine enough although it is true that, on the other hand, the error, as a possible result of removing the animals after taking them out, is smaller in a thicker sample.

Sampling sites

The investigated material was sampled from two different water-types: from the shallow, astatic saline „lakes“ and the river Tisza.

a) Saline lakes. Small stagnant waters in the region of Fülöpháza, with sandy-muddy bottom, bordered by macrovegetation, or partly covered:

Lake Hattyúszék: the open water of the lake is of 1.5 ha surface, maximum water depth is 1 m, astatic water. Its predominant group is: Ceratopogonidae.

Lake Zsírosszék: 20.9 ha surface. A lake of astatic type. Predominant group: Ceratopogonidae.

Lake Szappanszék: elongated, 1.5 km long, about 200 m broad, of 10.4 ha surface, astatic. Predominant group: Ceratopogonidae.

Lake Kondor: the lake is of 34.2 ha surface, of 1.5—2 m maximum water-depth, of non-astatic type. Its predominant group is: Chironomidae.

The collections were carried out in spring 1972 (May) and summer 1974 (July) (MEGYERI, 1975).

b) In the Szeged stretch of the river Tisza, between the river kilometer numbers of 166—176, the bottom samples were generally taken from the biotopes close to the riverside. Water-depth: between 0.5—6 m. Time of collection: 1967—1975, on a spring (May) and five autumn (September, October, November) occasions. On the autumn, the water-level was receding or stagnantly low (FERENCZ—CSOKNYA, 1973; FERENCZ, 1974a). The predominant group of the zoobenthos in the river-reaches investigated was: Oligochaeta.

Results

The taxon-groups, in the sequence of the decrease in their individual number, are:

Saline lakes: Ceratopogonida (2210)

Chironomida (79)

Coleoptera (28)

Diptera: Brachycera (8)

Tisza: Oligochaeta (1410)

Ephemeroptera: *Palingenia longicauda* (293)

Amphipoda (185)

Chironomida (96)
 Trichoptera (54)
 Diptera: Brachycera (49)
 Ceratopogonida (16)
 Polychaeta: *Hypania invalida* (14)

Oligochaeta. This is the predominant group of the river. The depth-distribution varied with the single collections. Their maximum generally falls into upper 10 cm, but it also occurs between 10 to 20 cm. Surface-dominance is about 50 per cent (Fig. 3) This datum differs from the results of other investigations of similar character (BRINKHURST, 1969), according to which more than 99 per cent of the worms were found in the 10 cm layer below the surface. With respect to the modifying effect of the life stage (differences in size, period of reproduction), we have no data concerning vertical distribution. According to BRINKHURST, the vertical distribution is not specific in Annelids. The maximum richness of the upper 2 cm layer (water -mud

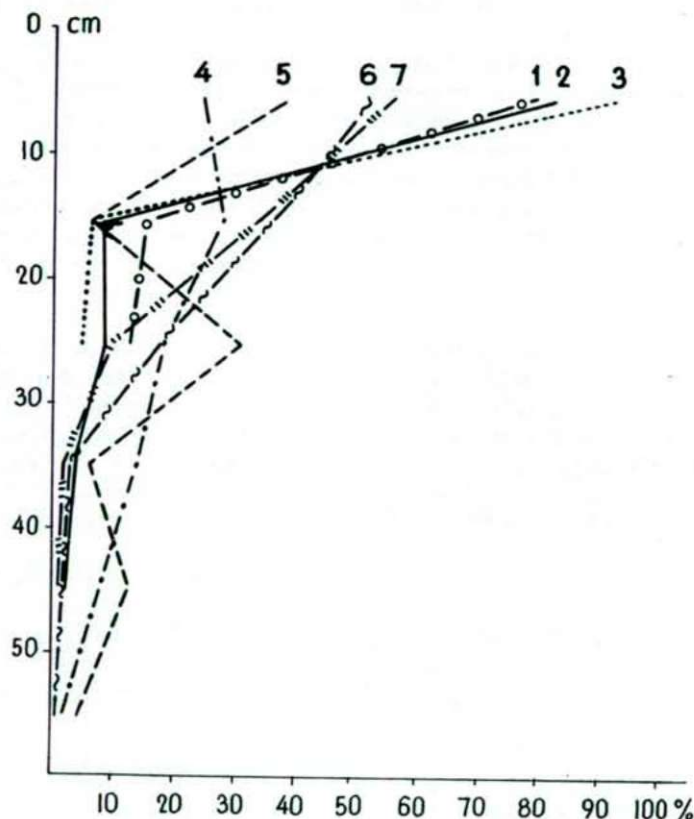


Fig. 1. Vertical distribution of zoobenthos in the Tisza, 1.: Polychaeta (*Hypania invalida*). 2.: Chironomida, 3.: Trichoptera, 4.: Ephemeroptera (*Palingenia longicauda*), 5.: Ceratopogonida 6.: Oligochaeta, 7.: Amphipoda.

interface) in individuals is explained by the above author as due to the respiratory mechanism of the animals, and the density of population of the 6 cm thick silt layer is also due to the large amount of heterotrophic bacteria living there, which serve as food. It is beyond question that, apart from some exceptions, the alimentary homogeneity of the fresh-water Oligochaeta species (detritophagous or bacteriophagous) can be established. In the four saline lakes investigated there were no Annelids.

Ceratopogonidae. The predominant group of the great majority of saline waters is formed by these detritophagous or predatory larvae. These thin-bodied, rapidly moving animals can exist even in the deepest layers of the bottom. Leaving the quantitative fluctuations at the beginning of collections out of consideration, their predominance in the upper layers can be established, and their percentage is fairly high at a 15–20 cm depth in natron lakes, as well as 20–30 cm deep in the river. (Figs. 2., 4). In this respect they differ from the behaviour of the other taxon-groups. Their larvae that tolerate even the extreme conditions well, putting up a stout resistance to the unfavourable effects, do not achieve high individual number in the river. Their vertical distribution takes, nonetheless, a similar form in both biotope-types.

Chironomidae. Their larvae showed a similar individual number and vertical distribution both in the river investigated and in stagnant waters. Their surface predominance is 80–85 per cent (Fig. 1). Most of them are detritophagous, and respond the quickest to the food-supply coming from the water (LELLÁK, 1965). The individual density of this group, — known as an important component of the zoobenthos, — is generally in inverse ratio to that of the Oligochaeta (LELLÁK, 1965; FERENCZ, 1974b). Many species of these make loose or rather stable dwelling-tubes. And those of them not having such tubes, can bore themselves into even greater depths in the bottom (50 cm).

Ephemeroptera. In the material investigated there was only a single mayfly species, *Palingenia longicauda*. The maximum individual number of its larvae, living in self-made ducts in the calyey riverside sectors was found at a 10 to 20 cm depth, although there was some fluctuation to be observed in the single collections in their vertical distribution (0 to 10, resp. 10 to 20 cm). It is an unequivocally detritophagous species, with a characteristic special biotope (CSOKNYA—FERENCZ, 1972). Its vertical distribution is influenced by its ontogeny and the change in the water-level.

Amphipoda. This is an essential group of the river zoobenthos from the point of view of both their individual number and their decomposing activity. They are detrito-, and necrophagous animals. Their vertical distribution is very similar to that of other Diptera taxon-groups. Their surface dominance is between 50–60 per cent. Their individual number decreases uniformly to the 50 cm depth.

Trichoptera. These species live dwelling tubes in the upper layers of the bottom. In the Tisza, their surface dominance is over 90 per cent. They can be characterized, therefore, as a typical surface group. Their depth-record is also the smallest, similar to the Polychaeta: *Hypania invalida*.

Polychaeta. This is a group represented by only,

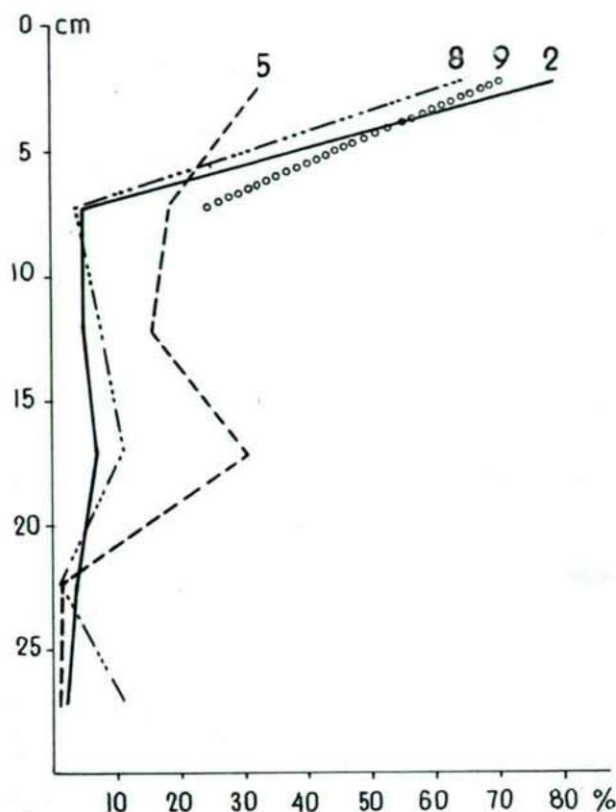


Fig. 2. Vertical distribution of zoobenthos in saline waters, 2.: Chironomida, 5.: Ceratopogonida, 8.: Coleoptera, 9.: Diptera (Branchycera).

Hypania invalida, a species immigrated from the Black Sea and living in the Tisza. It can probably even leave its loose mud dwelling-tube, much longer than its body. It can swim and dig itself into the bottom. It prepares its new dwelling-tube at the surface of the sediment. This is the taxon with the lowest individual number in the material investigated. Its vertical distribution is similar to that of the former group, being thus a typically surface member of the zoobenthos (FERENCZ, 1969).

Coleoptera. This is a group characteristic of some saline waters and achieving higher individual numbers from time to time. With respect to its vertical distribution, it could not be observed if the larvae or imagoes were closer to the surface, or in the deeper parts of bottom. The group takes a place in the sediment similar to that of the Chironomidae.

Diptera: (other). This group, achieving no individual number in any of the water-types, was represented by the Branchycera larvae.

The effect of the extreme water-level fluctuation, and drying on the vertical

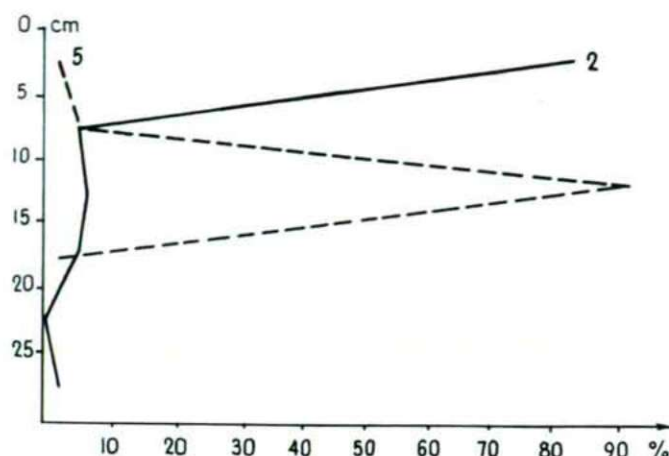


Fig. 3. Vertical distribution of zoobenthos in non-dried saline waters, 2.: Chironomida, 5.: Ceratopogonida.

distribution of the zoobenthos was studied in astatic saline lakes. While the Ceratopogonida-Chironomida group responded differently to the drying up of water, the Chironomida-Coleoptera groups showed certain similarity.

In water-covered places, the Ceratopogonida larvae tended to concentrate deeper in the bottom. On a wet, not completely dried out lake-bottom their individual number decreases in the deeper bottom layers and increases in the surface ones. On a dried up bottom, most larvae are in the upper 5 cm (Fig. 7).

The Chironomida larvae live in the upper layer of the water-covered bottom — and that is, of course, the typical case at the river, as well. They do not bear drying up well (their absolute individual number decreases). They withdraw into the deeper layers.

This antagonism between the Ceratopogonida-Chironomida groups has manifested itself in various ways in the course of my investigations.

That these characteristics of the vertical distribution, as a result of the extreme changes in the water-level, are not connected with the swarming of the two insect-groups, is proved by sampling at the same time but from different places.

If we are comparing the single groups on the basis of the surface dominance, of the maximum occurrence in depth — avoiding typization or categorization (we have too few data for these) — then it can be established that

a) those living at the surface of the bottom are: Trichoptera, Polychaeta, Chironomida,

b) those not living at the surface of the bottom are: *Palingenia longicauda*, Ceratopogonida.

About the half of the zoobenthos organisms live in the upper layer of the sediment-according to the data of our investigation. This seems to be but few as, from the point of view of food-supply and O_2 -content, the optimum situation exists in the upper layer. In waters with fish, however, fishes mean selection, consuming

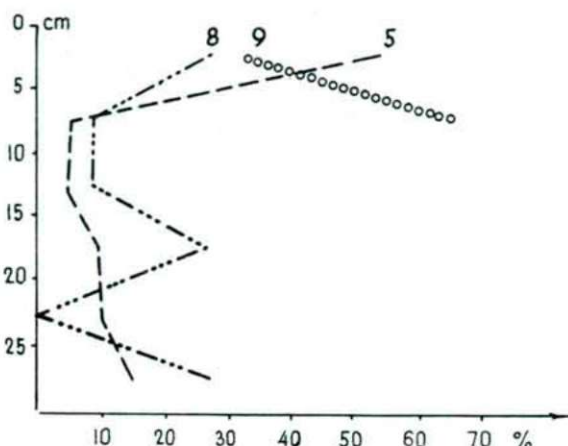


Fig. 4. Vertical distribution of the zoobenthos in dried saline waters, 5.: Ceratopogonida, 8.: Coleoptera, 9.: Diptera (Brachycera).

about half of the zoobenthos (LELLÁK, 1965). Nevertheless, on the basis of comparing the saline waters and the river Tisza from this point of view, the two water-types show no essential difference, although in the natron lakes there are no fish. The picture of the vertical distribution of the zoobenthos in case both water-types is probably so similar because of the greater individual density of the Ceratopogonida larvae a predominant group, as observed in the deeper bottom layers.

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FEEDING ACTIVITY AND REGULATING FACTORS OF *FORMICA PRATENSIS* RETZ (HYMENOPTERA: FORMICIDAE)

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Abstract

In the field the feeding activity was measured via the number of individuals leaving the colony in a 5-minute period, and in the laboratory via the movement between an artificially created polycalic colony and the feeding arena. In the seasonal activity a maximum is observed at the end of May and the beginning of June, while within a day the maximum activity occurs at 8—9 a.m. and around 2 p.m. The daily rhythm of the ants is induced by external factors; under laboratory conditions this rhythm is progressively lost.

Introduction

Elucidation of the daily and seasonal changes in feeding activity brings us nearer to an understanding not only of the ethological-ecological character of the given species, but also of the roles of matter and energy turnover in the ecosystem. A number of authors have earlier dealt with the study of the daily and seasonal activities of ants. BARONI—URBANI (1965, 1969) investigated the nocturnal activity changes of *Camponotus nylanderii*, and the daily rhythm of the activities of the coexistent *Lasius alienus* and *Tetramorium caespitum*. ABE (1971) studied the activity variations of the species *Formica japonica*, *Camponotus japonicus*, *Tetramorium caespitum* and *Messor aciculatus* with one-day observations on each species in August 1968. PETAL (1972, 1974) examined the feeding activities of *Myrmica laevinodis* and *Lasius niger* with Barber traps dug into the soil. GALLÉ (1972) used sugar baits in research into the correlation of the temperature and the feeding activities of *Lasius niger* and *Formica cunicularia*. NIELSEN (1972) studied the effects of meteorological factors on the aboveground activity of *Lasius alienus*. HUNT (1974) investigated the activities of *Tapinoma* and *Dorymyrmex*, and HEMMINGSEN (1973) that of *Oecophylla*.

For *Formica pratensis* in South Siberian steppe ecosystems, STEBAEV and REZNIKOVA (1972) observed an activity maximum at 6 p.m., while for the same species DLUSSKY (1967) found activity minima at 1 a.m., 6 a.m. and 2 p.m., and appreciable maxima at 8 a.m. and 2—3 p.m. He brought the daily rhythm in the activity into correlation with the temperature.

Materials and Methods

A study was made of a polycalic colony sited in a *Festucetum vaginatae salicetosum rosmarinifoliae* and *Astragalo-Festucetum sulcatae* plant association at the edge of a *Pinus silvestris* plantation. The ants largely went among the pine trees to feed, and thus, via their activity, created a material

turnover contact between the grassland and woodland ecosystems. Observations were made on 8 feeding routes; the ants leaving the nest and returning to it were observed and counted in 5-minute periods on the various routes, and at the same time the temperature and humidity at the soil level were measured.

The examinations were carried out in the 4 years 1971—1974. In 1971 and 1972 nets were erected above the nests to keep away woodpeckers; in 1973 these were removed, and in 1974 measurements were made of the decrease in the number of individuals due to the activity of the woodpeckers, mainly *Picus viridis* and *Dendrocopos major*.

Besides the field studies, a „model colony“ created in the laboratory was also investigated, in a relatively equilibrated climatic situation. The laboratory colony consisted of 3 nests, which were in contact with one feeding area. The nests, which were situated in glass baths with a base area of 20×30 cm, were connected to the feeding arena, with a base area of 0.5×1 m, via feeding routes constructed from wooden laths. The ant-food consisted of a mixture containing agar agar, sugar, honey, water and milk powder, which was cooked and a multivitamin mixture then added. Simultaneously with the laboratory daily activity observations, the temperature and humidity were also measured.

Results

The seasonal activity changes are depicted in Fig. 1. It can be seen that in both 1972 and 1974 the activity maximum occurred at the end of May and the beginning of June. As a result of the protection afforded by the nets, the number of individuals feeding in 1972 was several times that in 1974.

On sunny cloudless days, the daily activity pattern displayed two minima, at 4 a.m. and 11 a.m., and two maxima, at 8—9 a.m. and 2—3 p.m. (Figs. 2 and 3). In overcast weather the values of the maxima and minima were not so extreme.

The temperature and humidity measurements made in parallel with the observations of the changes in activity permit us to seek a correlation between the variations in the microclimatic factors and the feeding activity trends. If the feeding activity is plotted as a function of the temperature, a clear-cut correlation is not obtained for either the number of individuals leaving the nest ($r=0.2990$; $p>0.1$) or the number

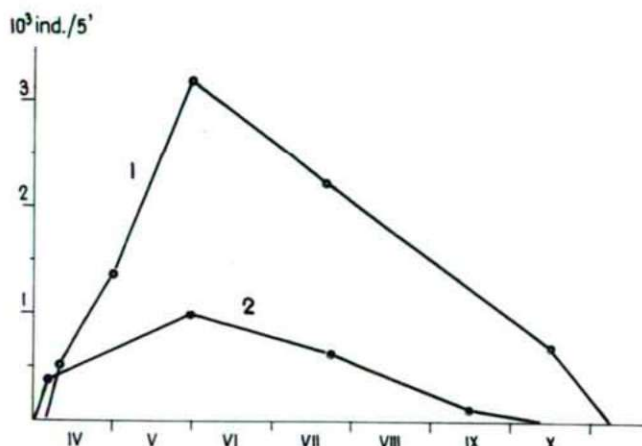


Fig. 1. Annual rhythm of feeding activity of *Formica pratensis*. The values given in the Figure are the average activities between 8 and 9 a.m. in the relevant seasons. Values observed in (1) 1972 and (2) 1974: numbers of ants leaving the nest during 5 minutes.

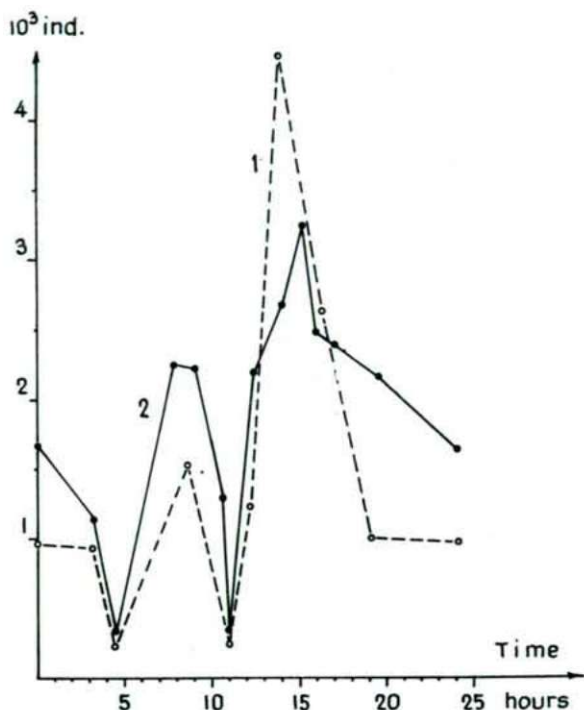


Fig. 2. Daily rhythm of the activity in the summer of 1972. (1) number of ants leaving the nest, (2) number returning to it, in a 5-minute period.

returning to it ($r=0.2063$; $p>0.1$) (Figs. 4 and 5). The activity threshold value however, can be established definitely (8–10 and 39–40 °C). Similarly as for the temperature, a clear-cut correlation was not obtained with the relative humidity either. Nevertheless, if a climogram plot is prepared, it emerges that the two micro-climatic factors together do determine the activity, for which a temperature of 28–35 °C and a relative humidity above 67% are optimum (Fig. 6).

In the laboratory a morning minimum could similarly be observed, at 10.30 a.m., with an early-afternoon maximum, between 12 a.m. and 2 p.m.; i.e. both occurred somewhat earlier than in nature. At the time of the examination the colony had been under laboratory conditions for more than 2 months, and it can be seen that by then the workers had largely lost their daily feeding rhythm: the values of the maxima and the minima were much less extreme than under natural conditions (Figs. 7 and 8).

Discussion

In the course of his observations on *Formica pratensis*, DLUSSKY (1967) found that the activity is affected by the temperature alone, the optimum being around 20 °C, i.e. essentially lower than that found in our measurements. A further differ-

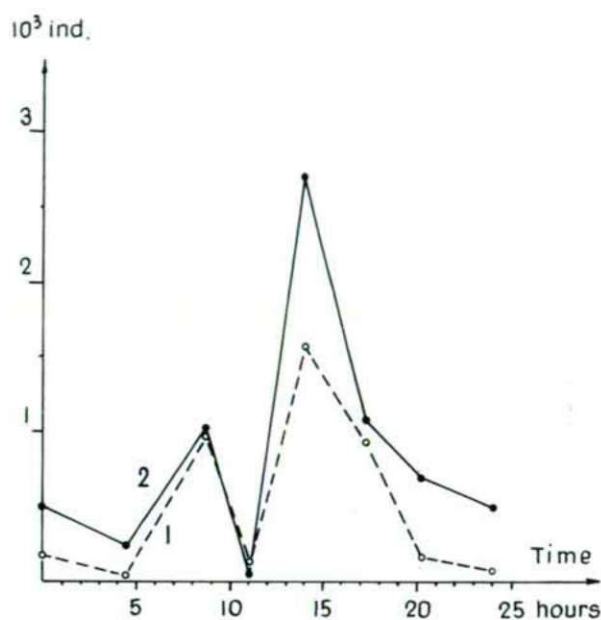


Fig. 3. Daily rhythm of the activity in 1974. Notations as in Fig. 2.

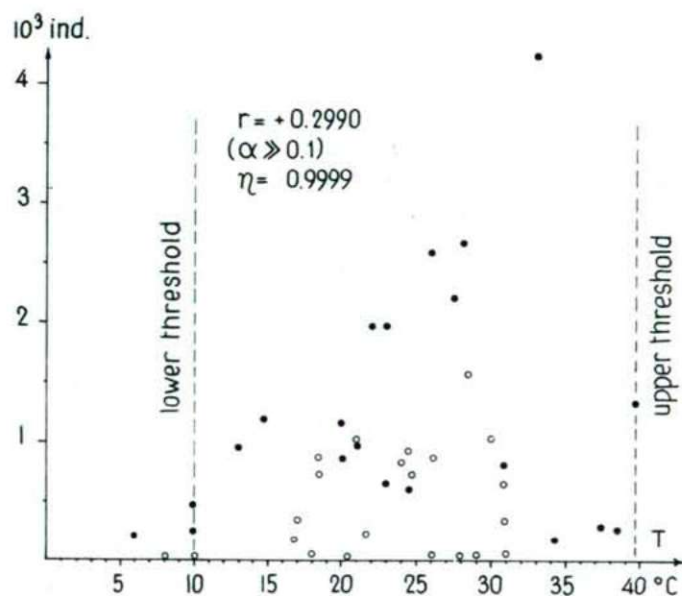


Fig. 4. Connection of the temperature and the number of ants leaving the nest. 1971-1972: dark points; 1974: circles.

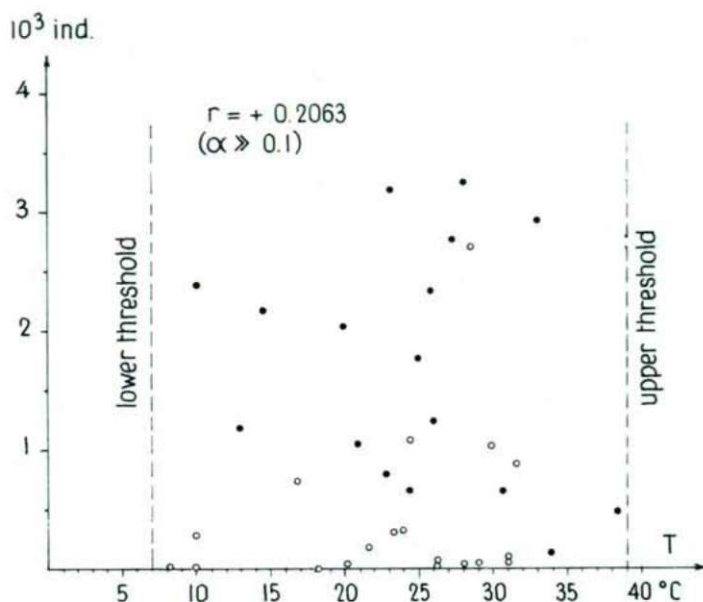


Fig. 5. Connection of the temperature and the number of ants returning to the nest.

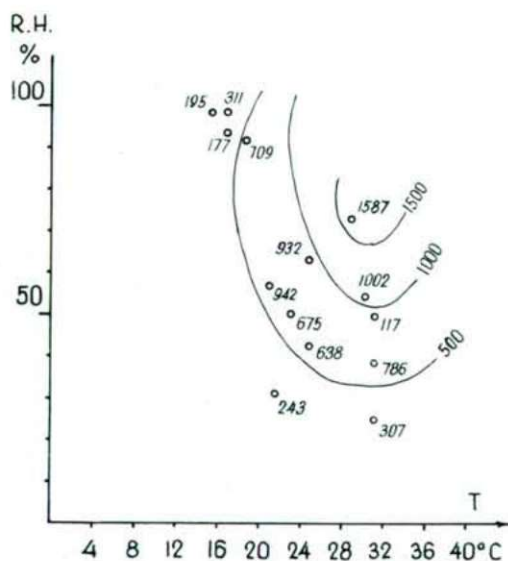


Fig. 6. Activity climogram of ants leaving the nest in 1974, with some critical experimental data.

ence between the two results is that our measurements did not reveal such a clear-cut correlation between the temperature and the activity as did those of DLUSSKY. However, our examinations fully support the finding of DLUSSKY that whereas the

regulating factors have a clear effect on the number of outgoing individuals, as seen in Fig. 6, the well-fed individuals returning to the nest generally react only after some delay to changes in the microclimatic factors.

The field climate-chamber measurements of NIELSEN (1972) did not reveal a daily rhythm in *Lasius alienus* in a constant climatic situation. On the basis of our present examinations, it may be assumed that a rhythm develops in the workers of *Formica pratensis* in accordance with the daily periodic changes in the environmental factors (temperature, humidity), but that under altered conditions in the laboratory this rhythm is gradually lost. That the rhythm involved is not of endogenous origin, but is induced by external conditions, is supported by the fact that the daily cycle of nests of this species develops in a different way in a different environment (STEBAEV and REZNIKOVA, 1972).

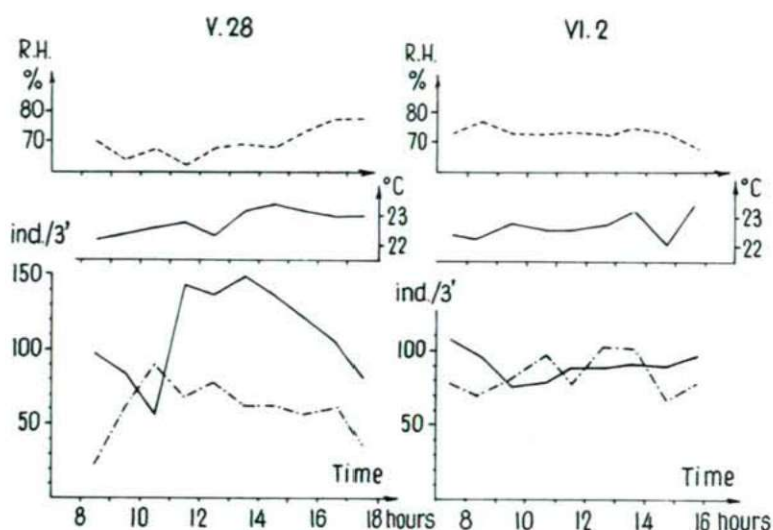


Fig. 7—8. Laboratory temperature and humidity, and daily rhythm of laboratory colony. (1) number of ants on feeding routes during 3 minutes; (2) number of ants on routes between nests during 3 minutes.

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PREDATORY INSECT POPULATIONS IN THE HOST-PLANT COMMUNITY OF THE RED PEPPER (CAPSICUM)

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Abstract

The host-plant community of the red pepper (*Capsicum*) was investigated from 1971 to 1973. The food of *Orius niger* WOLFF is: aphids, Acaridae, and *Empoasca fabae* HARR. These Hemiptera lay their eggs in the parts of the flowers, and this is harmful. Apart from the species *Coccinella septempunctata* L. and *Adonia variegata* GÖEZE, *Nabis feroides* REM. also occurred every year. The propagation of *Chrysopa* species and Syrphidae larvae is linked to cool, wet weather, while the changes in the individual numbers of spiders depends less upon abiotic factors.

Introduction

An effective defence against the insect populations damaging the red pepper may be to employ insect predators. In the literature, only the predators of aphids have been dealt with so far. From among these, the major species mentioned from the Coccinellidae family are: *Coccinella septempunctata* L., *Adalia bipunctata* L., and *Chilocorus* sp. (SZALAY—MARZSÓ, 1961). These species are efficient mainly in the estival phase, for at this time the aphid nymphs are not yet being looked for by parasites. However, they are destroyed by the predatory *Coccinellida* larvae (STARY, 1972). The first two Coccinellidae have been examined with regard to biological protection against *Myzus persicae* SULZ, and it was found (GURNEY—HUSSEY, 1970) that the insects were more voracious at a lower temperature than at a higher one. As a result of the activity of *Coccinellida* populations, the aphids may disappear completely from the paprika fields, e.g. in 1957 when there occurred even ten larvae of *Coccinella septempunctata* L. on each paprika plant (SOLYMOSEY—SZALAY—MARZSÓ, 1959). On a small plot of land, *Chrysopa* spp. was a more efficient predator than *Coccinella septempunctata* L. against a medium or low aphid contamination (SHANDS—SIMPSON—STORCH, 1972). Of the species of the Syrphidae family, *Epistrophe balteata* DEG., *Sphaerophoria scripta* L., *Syrphus lunulatus* MEIG., *Syrphus ribesii* L., and *Chrysotoxum intermedium* MEIG. have also been mentioned as predators (SZALAY—MARZSÓ, 1969). In 1957 *Epistrophe balteata* DEG. predominated in Szeged (SOLYMOSEY—SZALAY—MARZSÓ, 1969). The activity of the larvae and imagoes of Anthocoridae was regarded as important only against the aphids of fruit-trees (SZALAY—MARZSÓ, 1969). Spiders are important only in the period of hatching of the aphid fundatrices (REMAUDIERE—LECLANT, 1971).

Materials and Methods

The soil of the area investigated, a condiment-paprika field 23.6 ha in size in the environs of Szeged, was carbonate meadow chernozem on the surface. The paprika (*Capsicum annuum* L. convar. *longum*) was planted in rows at 60 cm intervals, with 60 cm (possibly less) between plants. In 1971—1973, insect nets were used for collections from the individual plants, according to the „hundred plant“ method (SZALAY—MARZSÓ, 1969). 5×20 plants were generally netted on each occasion. The material was separated after ether anaesthesia. The mean daily temperature values were obtained from the meteorological station beside the collecting area. Collections were generally made in the morning hours, on one occasion a week.

Results

As regards the predatory populations, *Aeolothrips intermedius* BAGN., not mentioned in the literature, was conspicuous with the highest number of individuals. This species will be dealt with elsewhere.

The Anthocoridae family was represented by two species, *Orius niger* WOLFF. and *Orius majusculus* RENT. In 1971, *Orius majusculus* RENT. constituted 22 per cent, and in 1972 11.3 per cent, while in 1973 its ratio was insignificant: the data on it are therefore given combined (Figs. 1—3). It turns out from the data for all three years that plant-bugs begin breeding in early July. A cause of this is that plant-bugs not only find their food in red pepper but also lay their eggs in the flowers. As seen from the data for 1971, blooming begins from the end of July. Before this, a few flowers can be found. Eggs were found in the most various parts of the flowers:

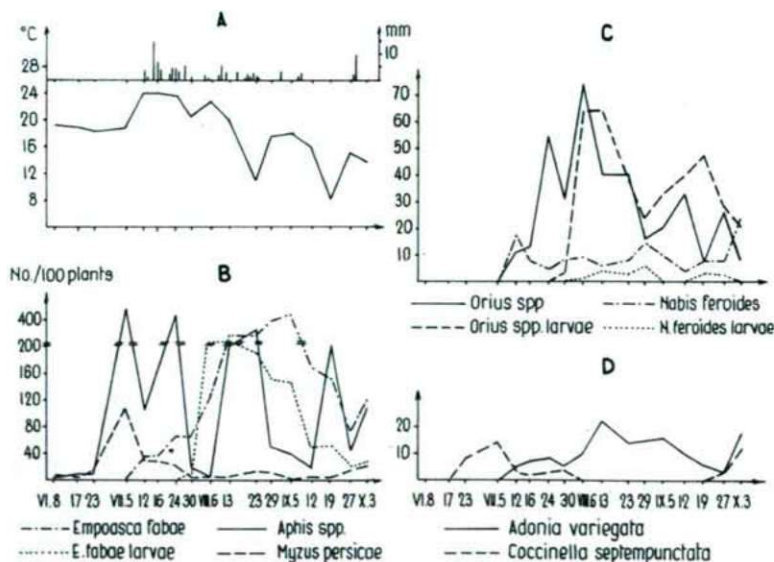


Fig. 1. a) Mean daily temperature and precipitation values in 1971.

b) The main plantivorous populations in 1971.

c) Predatory populations in 1971, I.

d) Predatory populations in 1971, II.

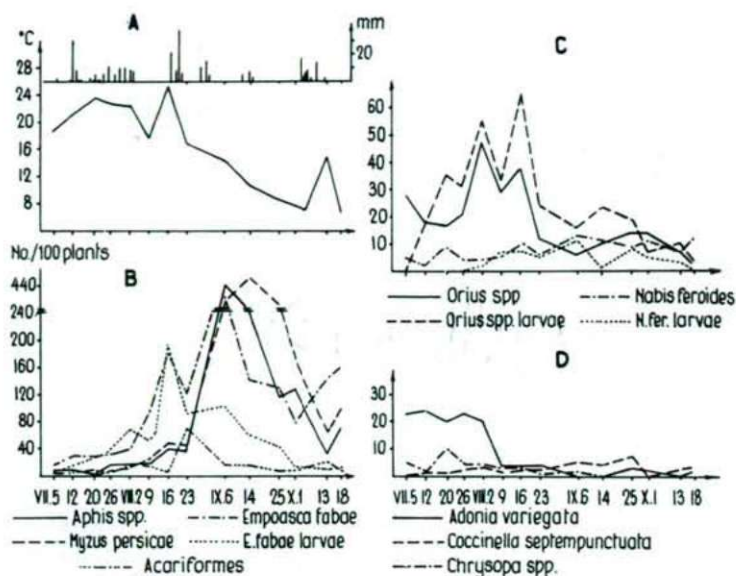


Fig. 2. a) Mean daily temperature and precipitation values in 1972.
 b) The main plantivorous populations in 1972.
 c) Predatory populations in 1972, I.
 d) Predatory populations in 1972, II.

petal, filament, and pollen sacs. In one flower there occurred as many as 3 to 5 eggs, impeding the fastening and formation of the crop.

Until the red pepper is suitable for plant-bugs, they can be found in the borderland, with low individual density. After it has become suitable for them, they migrate almost completely onto it. In favourable warm weather, the plants become populated with bugs already in June. Two generations develop a year, following one another at an interval of about forty days.

After egg-laying, depending upon the blooming, the larvae are hatched in about eight days. Their development, and size of the population are strongly temperature-dependent. The individual density maxima coincide with the mean temperature maxima.

The mean-temperature curves in 1971 and 1972 exhibit a striking parallel with the individual-density curves.

The population is considerably reduced by a decrease in temperature and by rainfall, even if the quantity of food-animals is large (e.g. August 23, 1971). The main food of bugs is aphids, with mites as second favourite but *Empoasca fabae* larvae are not rejected either. This shows up in the high individual density in August 1971, which cannot be explained on the number of aphids: the larva-population of *Empoasca fabae* Harr. joined the community here. The initial propagation of aphids could not be impeded by bugs. Later too, the activity of these is considerable only above a daily mean temperature of 10 °C. Because of their thermophilous nature, they can be of importance only from middle July to late August. In the course of the three years, the conditions were more favourable for *Orius niger* WOLFF. *Orius majusculus* RENT.

was driven more and more into the background. The activity of *Nabis feroides* REM. also had to be taken into consideration every year (Figs. 1—3). This species is a polyphagous enemy of Herbivores. It survives the winter in a fully-developed form. Its eggs are laid on the first spring days, mainly in the tissues of clover, wheat and other cereals (BJEGOVIC, 1968). The imagoes were active in the borderland already in March. Larvae appeared in early June; the generation developing out of these migrated onto the red pepper from late June. *Nabis* likes to lay its eggs on the inner surface

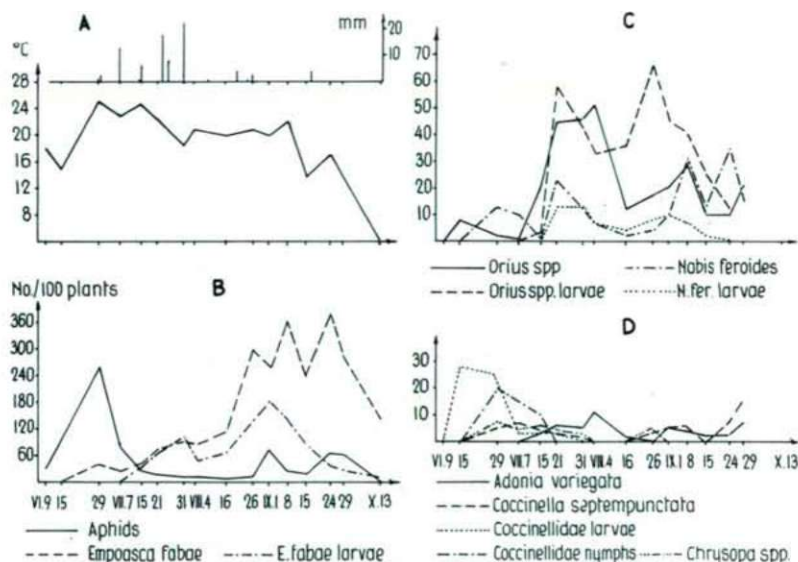


Fig. 3. a) Mean daily temperature and precipitation values in 1973.
b) The main plantivorous populations in 1973.
c) Predatory populations in 1973, I.
d) Predatory populations in 1973, II.

of the petals. The larvae also stay in the flowers for a long time. The larvae of the second generation (on the pepper the first one) are hatched in the middle of July. The plant-bug is not linked to any food-animal exclusively.

On the red pepper, two species of the Coccinellidae family predominated: *Coccinella septempunctata* L. and *Adonia variegata* GÖEZE; in addition, in 1972, *Hyppodamia 13-punctata* L. and *Halysia 14-punctata* L. appeared. The insects can be found in the borderland already in early spring. First, *Coccinella septempunctata* L. migrates to the paprika, followed two weeks later by *Adonia variegata* GÖEZE. The time of migration, its intensity, and the propagation of the insects depend mainly upon the quantity of food-animals (aphids). It was therefore possible in 1973 to find a large number of eggs already on May 26. *Coccinella septempunctata* L. prefers to consume *Myzus persicae* SULZ., while *Adonia variegata* GÖEZE prefers *Aphis craccivora* KOCH. The overpropagation of aphids can only be impeded if first of all the individual density is depressed to a duly low level. After spraying on July 6,

1973, the predators already proved to be sufficient for preventing the aphids from mass multiplication.

The multiplication of *Chrysopa* species (*Chrysopa carnea* STEPH., *Chrysopa ingens* STEINM.) is promoted by cool, rainy weather. It is therefore worthwhile to mention them only for 1972, because the weather was then particularly rainy.

In the case of the larvae of the Syrphidae the situation is similar. They appeared in large numbers only in 1972, and even then only in the middle of September, at a mean temperature of 10 °C, accompanied by a high humidity (Fig. 2).

The representatives of the Araneidea group appear with similar individual density every year (Fig. 4). Their number rose from the middle of June uniformly,

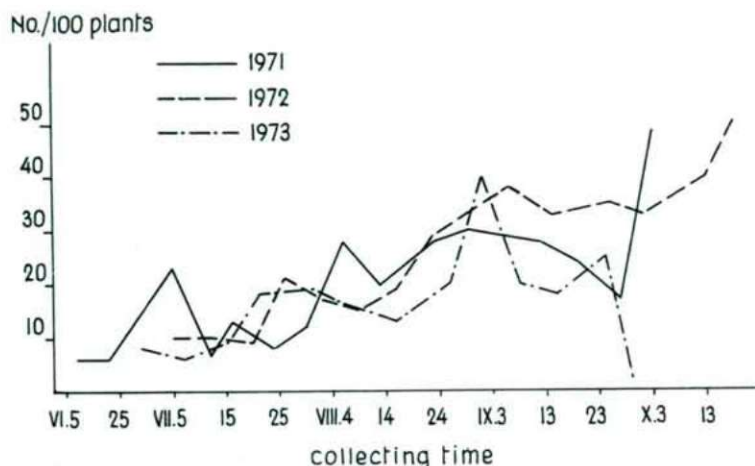


Fig. 4. Changes in the individual densities of Araneidea spp. in 1971—1973.

Table 1. Predatory populations in 1971.

Species No./100 plants	June				July				August				September				October
	8	17	23	5	12	16	24	30	6	13	23	29	5	12	19	27	3
<i>Orius niger</i> WOLFF.	—	—	—	—	11	9	47	20	42	36	36	14	17	38	7	23	8
<i>Orius majusculus</i> RENT.	—	—	—	—	—	4	7	11	32	4	4	2	3	—	1	3	—
<i>Orius</i> spp. larvae	—	—	—	—	—	—	—	—	3	64	64	38	24	33	40	47	20
<i>Nabis feroides</i> REM.	—	—	—	—	17	8	5	8	9	6	8	14	10	4	—	8	24
<i>Nabis feroides</i> REM. larvae	—	—	—	—	—	—	—	—	1	4	2	6	—	—	3	2	—
<i>Coccinella septempunctata</i> L.	—	—	8	14	3	2	3	4	—	—	—	—	—	—	—	3	12
<i>Adonia variegata</i> GOEZE.	—	—	—	—	5	7	8	5	10	22	14	14	16	10	6	3	18
<i>Chrysopa</i> spp.	—	—	—	2	—	1	3	1	—	—	—	4	—	—	—	—	—
Araneidea	8	6	6	23	7	13	8	12	28	20	28	30	29	28	24	17	44

Table 2. Predatory populations in 1972

Species No./100 plants	July				August				September			October		
	5	12	20	26	2	9	16	23	6	14	25	1	13	18
<i>Orius</i> spp.	28	18	17	21	47	29	38	12	6	10	14	14	7	2
<i>Orius</i> spp. larvae	—	17	35	31	55	33	65	24	16	23	19	7	10	3
<i>Nabis feroides</i> REM.	5	3	9	4	4	5	10	6	13	11	10	11	7	12
<i>Nabis feroides</i> REM. larvae	—	—	—	—	2	6	7	5	11	1	9	5	3	—
<i>Coccinella septempunctata</i> L.	—	1	1	2	3	1	2	1	5	4	7	—	2	2
<i>Hyppodamia 13—punctata</i> L.	—	—	—	—	3	2	1	1	—	4	—	—	1	—
<i>Halyzia 14-punctata</i> L.	5	—	—	3	1	2	4	3	2	3	4	4	—	2
<i>Adonia variegata</i> GOEZE.	23	24	20	23	20	4	4	4	—	—	3	2	—	2
Coccinellidae larvae	—	—	—	—	—	—	—	—	2	—	14	7	7	5
Chrysopa spp.	5	2	10	5	4	4	4	1	1	—	—	—	—	—
Araneidea	10	10	9	21	17	15	19	29	38	33	35	33	40	50

Table 3. Predatory populations in 1973

Species No./100 plants	June			July				August			September				
	9	15	29	7	15	21	31	4	16	26	1	8	15	24	29
<i>Orius</i> spp.	—	8	2	1	20	45	46	51	12	17	20	28	10	10	21
<i>Orius</i> spp. larvae	—	—	—	—	3	58	41	33	36	66	45	41	25	12	20
<i>Nabis feroides</i> REM.	—	—	13	10	1	23	12	7	2	4	10	31	13	35	15
<i>Nabis feroides</i> REM. larvae	4	—	—	—	—	13	13	7	4	8	10	7	2	—	—
<i>Coccinella septempunctata</i> L.	—	—	5	7	3	1	1	—	—	3	5	6	—	7	15
<i>Adonia variegata</i> GOEZE.	—	—	—	—	3	6	5	11	1	—	5	4	2	2	7
<i>Halyzia 14-punctata</i> L.	—	—	—	2	3	—	—	—	1	—	—	2	3	2	—
Coccinellidae larvae	—	28	25	3	3	1	—	—	—	—	—	2	2	2	—
Coccinellidae nymphs	—	—	20	10	15	—	—	—	—	—	—	—	—	—	—
Chrysopa spp.	—	—	7	4	6	4	3	—	—	5	—	—	—	—	—
Araneidea	—	—	8	6	9	18	19	17	13	20	40	20	18	25	2

achieving its maximum in early September. The cause of the rise in October, 1972 was the mass multiplication of flying insects (mainly *Scaptomyza pallida* ZETT., and *Oscinella frit* L.). The dynamics of spiders follows the individual densities of other insects well. Their multiplication is scarcely influenced by weather factors.

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DAS NEST VON *BOMBUS ALTICOLA* KRIECHBAUMER (HYMENOPTERA: APIDAE)*

L. MÓCZÁR

Aus dem Zoologischen Institut der Universität Szeged

(Eingegangen am 30. Juni. 1976)

Verfasser berichtet über die Nistverhältnisse und den Blütenbesuch der boreo-alpinen Art *Bombus alticola* KRIECHBAUMER, beschreibt die Larve, den Nestbestand samt den dort aufgefundenen Parasiten *Psithyrus rupestris* (F.) und *Mutilla europaea* L.

Die boreo-alpine Art *Bombus alticola* KRIECHBAUMER wurde bisher ausschliesslich in den Alpen und Pyrenäen gesammelt und über ihre Nistverhältnisse sind keine Angaben in der Literatur auffindbar. Es gelang Verfasser den Flug einer *Cirsium spinosissimum* Nektar sammelnden Arbeiterin verfolgend in dem südlichen Teil Ötztaler Alpen, auf dem Grüneben (Feld. Nr. 7) neben Obergurgel (Österreich: Tyrol) in einer Höhe von 1980 m am 26. 8. 1975 das Nest zu entdecken. Nach einigen Tagen befanden sich wegen der kühlen Witterung mit Schneeregen die Hummeln fast vollzählig in ihrem Nest, an den umgebenden Bergwiesen konnten Hummeln nicht beobachtet werden. Nun gelang es zusammen mit Herrn A. AICHHORN die 30 cm dicke Bodenschicht je Rasenziegel so zu entfernen, dass es nach der Aufnahme des Nestinventars diese in ihre ursprüngliche Lage zurückgelegt werden konnte.

Das Flugloch war durch hohes Gras verdeckt und der Gang führte mehrmals fast rechtwinkelig gebogen und dann unter zwei flachen Steinen in einer Gesamtlänge von 78 cm in das den Hohlraum ausfüllende Nest. Das Nest war mit einem dicken, dichten Schicht von Grasmüll umgeben. Die gegen das Nestinnere gekehrte Seite war mit Wachs zusammenge kittet.

Das Nest bestand aus folgenden Bauteilen:

1. 12 Puppenzellen mit Hummelpuppen (eine Puppe noch nicht geschlüpft) + 3 *Mutillazellen* (bereits geschlüpft)
2. 15 Zellen + eine *Mutilla* (noch nicht geschlüpft)
3. 4 Zellen + 3 *Mutilla* (geschlüpft)
4. 12 Zellen + 6 *Mutilla* (davon drei geschlüpft, 3 Weibchen noch nicht geschlüpft)
5. 11 Zellen + 6 *Mutilla* (noch nicht geschlüpft)
6. 2 Eibecker mit lebendigen Eier + ein kleiner Hügel mit 5 Larven.
7. 11 Larvenzellen, ihre Fabre war aber dunkelbraun und auch über die Larven war keine Decke gesponnen worden, drei grosse und 5 kleinere Larven konnte ich herausnehmen.

* Mit Unterstützung der Alpinen Forschungsstelle Obergurgl der Universität Innsbruck

8. 29 Männchen, 4 Weibchen und 2 Psithyrus Puppenzellen, diese zum Teil geöffnet liessen sich 4 Larven und 2 weibliche Puppen, ferner eine schwarze, entgetrocknete, verhungerte Arbeiterin finden.
9. In 14 kleinen Zellen Arbeiterinnen, unter diesen habe ich 4 tote Arbeiterinnen herausgenommen + ein *Mutilla*-Männchen + 1 weitere *Mutilla* (noch nicht geschlüpft).
10. 11 Wachshüllen, die zur Speicherung von Nektar und Pollen verwendet wurden.

Im Nest war zwischen den Zellen Pollen nichtmehr zu finden, offenbar wegen der vorangegangenen, zwei Wochenlang anhaltenden kühlen regnerischen Witterung, ja sogar Nektar konnte nur am Nestgrund, in zwei bedeckten, verlassenen Tonnen gefunden werden. Im Nest befanden sich: 36 *Bombus* Arbeiterinnen, zwei junge Weibchen, ein *Psithyrus rupestris* F. (Weibchen) und ein Männchen von *Mutilla europaea* L. An den *Bombus* Individuen, in den Wachszellen und im Grasmüll befanden sich unzählige Milben (Acarina) (*Tyrophagus laevis* [DUJARDIN] det. S. MAHUNKA) und viele winzige Coleopteren (*Cryptophagus scanicus* L. det. S. ENDRÖDY).

Beschreibung der Larve: der Körper besteht aus 13 Körper- und einem Kopfsegment. Die Farbe ist weiss, nur die Stigmen, die Cuticularvorwölbungen und der Kopf der vollentwickelten Larve ist grösstenteils braun. Die noch pollenfressenden Larven sind bogenförmig, die vollentwickelten halbkreisförmig gekrümmt. Bei dieser Lage erreichen die Mundteile das letzte Bauchsegment (Tafel I. Abb. 1). Die 10 Paar Stigmen befinden sich seitlich an dem vorderen Teil der Segmente 2—11 und sind gut sichtbar (Abb. 5) Die Cuticularvorwölbungen der Segmente 1—2 sind auf der Dorsalseite gut entwickelt und von brauner Färbung (Abb. 3). Dieselben auf Segment 3 sind kaum wahrnehmbar, nur schwach entwickelt und nicht braun gefärbt.

Der Kopf (Abb. 1) ist fast so breit wie lang, in der Mitte, zwischen der Stelle der zukünftigen Augen mit Spuren einer schwachen Furche. Kopfschild deutlich breiter als lang, sein Unterrand ziemlich gerade, mit der Oberlippe verwachsen. Oberlippe dreimal so breit wie lang, der Unterrand leicht ausgerandet, die Seiten konvergent, die Ecken breit abgerundet. Die Oberkiefer sind mächtige, gut entwickelte Chitingebilden mit scharfen Zähnen (Abb. 2). Die Unterkiefer befinden sich bei-

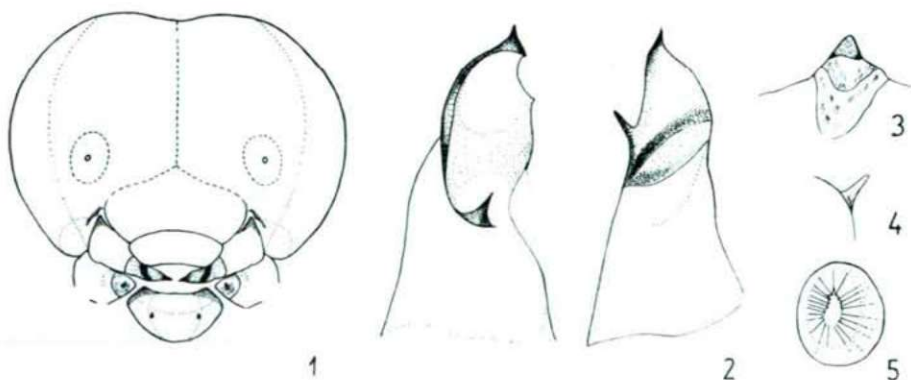
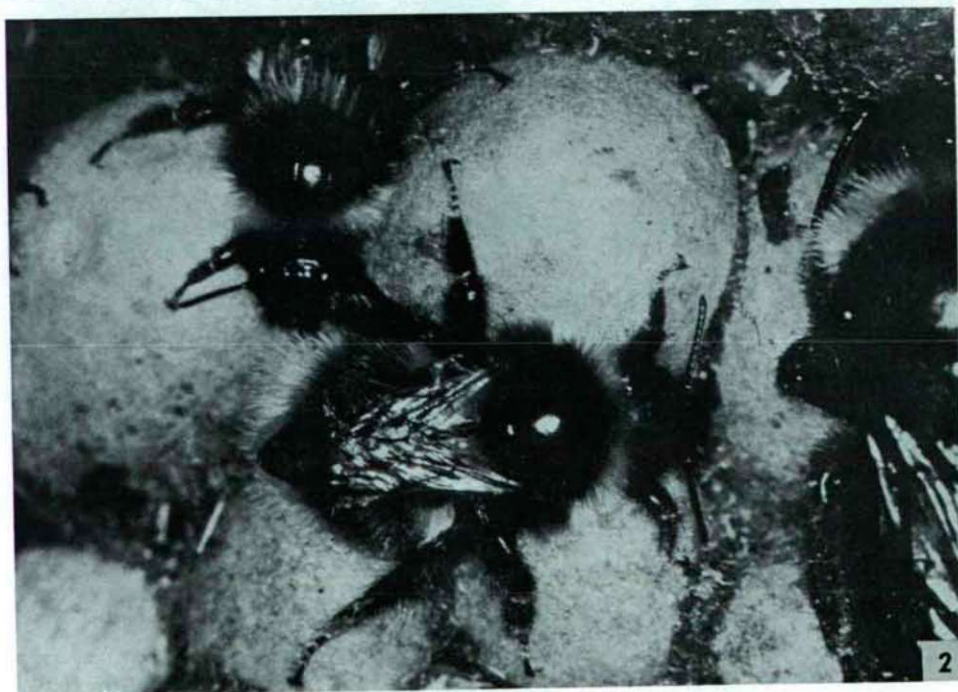
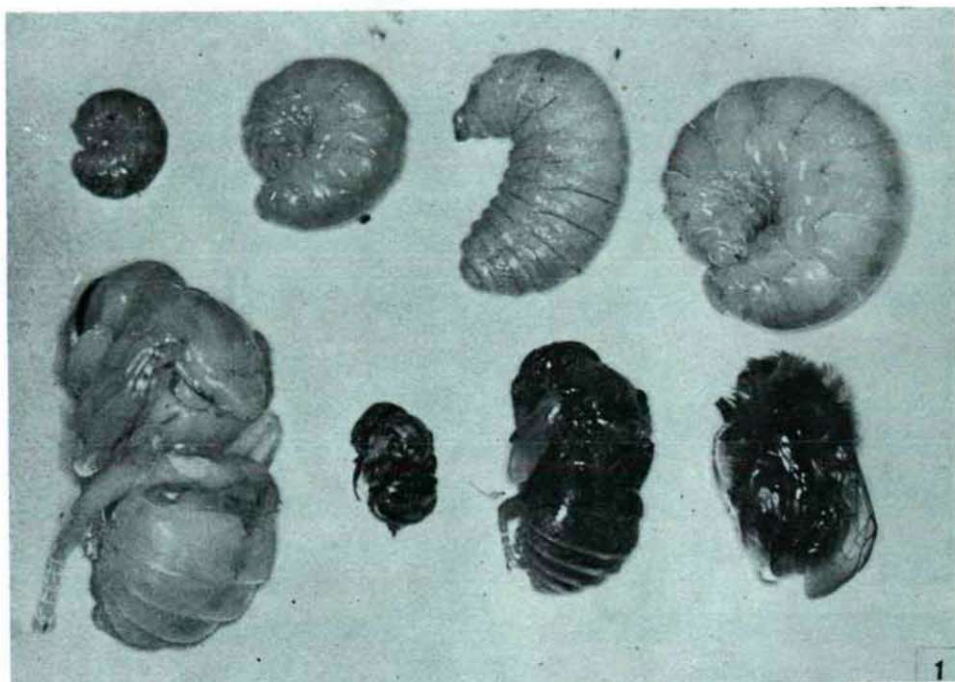
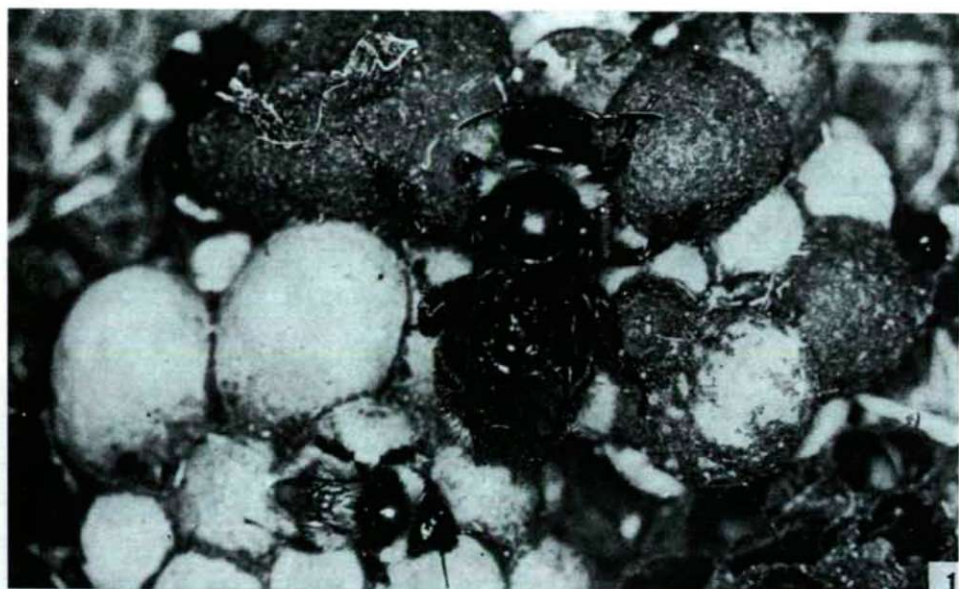


Abb. 1—5. Larve von *Bombus alticola* KRIECHBAUMER, 1: Kopf der Larve, 2: Oberkiefer, 3: Cuticularvorwölbung auf Segment 1, 4: Chitinhöckerchen, 5: Stigma. (Zeichn. A. FAZEKAS)

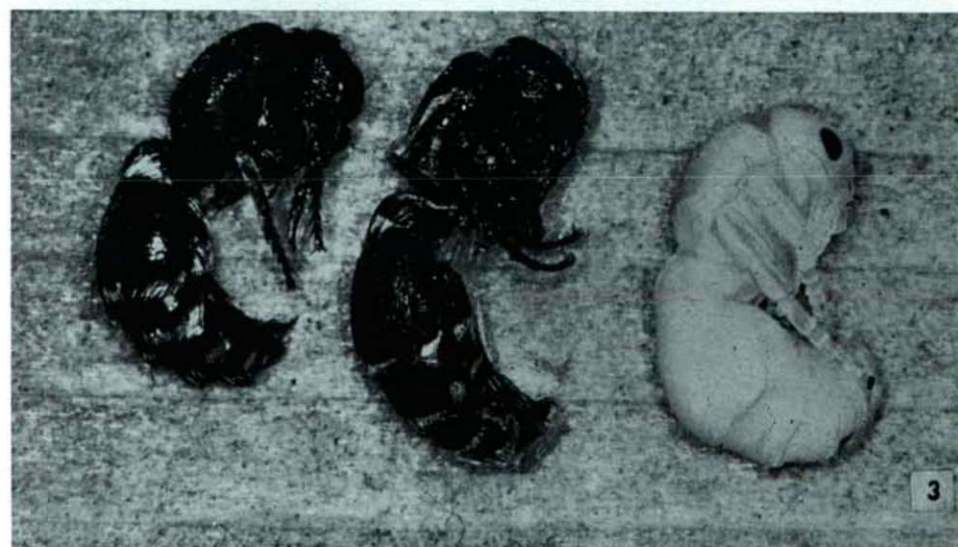


Tafel I. Abb. 1. Larven und Puppen verschiedenen Entwicklungsstadiums von *Bombus alticola* Kriechbaumer.
Abb. 2.: Die Arbeiterin erwärmen die Puppenzellen. (Orig.)



Tafel II. Abb. 1. Das Nest von *Bombus alticola* KRIECHBAUMER mit dunkel gefärbten Eibecher und Larven enthaltenden Häufchen, darunter die Puppen enthaltenden, hellen Zellen, in der Mitte der Schmarotzer *Psithyrus rupestris* (F.). Weibchen, rechts in der unteren Ecke leere und zu Aufbewahrung von Nektar dienende Zellen, im Nest betätigen sich einige *B. alticola* Imagines.

Abb. 2. Der Schmarotzer *Psithyrus rupestris* (F.) Weibchen im Nest von *Bombus alticola* KRIECHBAUMER, auf den Puppenzellen. (Orig.)



Tafel III. Abb. 1—3. *Mutilla europaea* L., 1: Männchen, 2: Weibchen, 3: Puppen verschiedenen Entwicklungsstadiums. (Orig.)

derseits unter den Mandibeln und sind einem fingerförmigen Zapfen ähnlich. An der Spitze trägt ein jeder ein Chitinhöckerchen (Abb. 4). Die Unterlippe ist breit und liegt unter den zwei seitlichen Unterkiefern, in der Mitte mit einer queren Spalte und seitlich unten mit zwei Chitinhöckerchen. An der Stelle der Fühler befindet sich eine schwache Cuticularvorwölbung.

Auf Grund der oben angeführten kann einwandfrei gefolgert werden, dass in dem mittelmässig bewohnten *Bombus alticola* KRIECHBAUMER Nest das nestgründer Weibchen nicht anwesend war, dort sich aber ein *Psithyrus rupestris* (F.) betätigte und sich viele Schmarotzer (*Mutilla europea* L. und *Ps. rupestris* [E.]) entwickelten. Das die Familie gründende Weibchen wurde wahrscheinlich wenige Tage vorher aus dem Nest vertrieben und verendete irgendwo draussen, weil seine Eier in der Baute Nr. 6 noch nicht zu Larven entwickelt waren (vorausgesetzt, dass die Eier nicht von dem *Psithyrus* Weibchen abgelegt waren). Auf das gesamte Nest wartete übrigens spätestens um Ende August das Aussterben, weil während der vorangegangenen zwei Wochen die ungünstige Witterung den pollen- und Nektarvorrat aufzufüllen nicht zuliess. *B. alticola* KRIECHBAUMER verfertigt sein Nest in einem unterirdischen Hohlraum, in etwa 30 cm Tiefe unter der Bodenoberfläche. Um Nektar zu sammeln besucht die Biene *Cirsium spinosissimum*. Seine Schmarotzer sind *Psithyrus rupestris* (F.), *Mutilla europaea* L., Kommensalisten Acarinen (*Tyrophagus laevis* DUJARDIN) und Coleopteren (*Cryptophagus scanicus* L.).

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ANTHROPOLOGICAL OUTLINES OF THE PREHISTORY OF THE SOUTHERN PART OF THE GREAT HUNGARIAN PLAIN AND OF NORTHERN JUGOSLAVIA

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Abstract

The results achieved by the author with respect to the Neolithic, Copper, and Bronze Ages in the Southern Part of the Great Hungarian Plain and Northern Yugoslavia are summarized on the basis of 1292 prehistoric anthropological finds from the above mentioned archaeological ages. The investigations were of metrical, morphological, palaeopathological, palaeodemographical, taxonomical character.

This work is the first attempt to interpret the development of prehistoric populations within a geographical unit of Hungary on the basis of extensive palaeoanthropological material.

Scientific antecedents

In Hungary extremely rich prehistoric archaeological and anthropological material has been found. The systematical evaluation of the archaeological finds was carried out and the results were published (BANNER, 1932, 1937; BÓNA, 1961, 1965, 1965a, 1966, 1975; KALICZ, 1970; B. KUTZIÁN, 1972; TROGMAYER, 1963, 1967, 1968, 1975). The same does not apply, unfortunately, to the skeletal material unearthed. Looking over the existing literature on the prehistoric anthropology of the whole Hungary, the following can be said.

From among the neolithic finds in this country there were, so far, made known: a single female find uncovered in the cave Bűdöspeszt (BARTUCZ, 1916), the graves at Békés—Povádzug (LIPTÁK—FARKAS, 1967), the finds of the cemetery at Lengyel (VIRCHOW, 1890; MALÁN, 1929), the find from Vaskút (NEMESKÉRI, 1944), the skeletons excavated from a hill at Vésztő—Mágor (FARKAS, 1974), the finds from Villánykövesd and Zengővárkony (K. ZOFFMANN, 1971, 1974), as well as the skeletons of the findspot Kisköre—Gát (TÓTH, 1972, 1973). The finds trephined from Lebő, Szentés—Ficsorhalom and Veszprém were treated by BARTUCZ separately (BARTUCZ, 1966). Finally, an earlier comprehensive survey of the Neolithic Age is also to be mentioned (BARTUCZ, 1938).

The number of finds published from the Neolithic Age is about 130. The 26 finds treated in the present work are to be added to these.

From among the findspots from the Copper Age, the anthropological evaluation was performed in the following cases: Alsónémedi (NEMESKÉRI, 1951), Budapest Andor street (NEMESKÉRI, 1956), Bodrogkeresztúr, Pusztaitvánháza (BARTUCZ, 1938), Csongrád—Kettőshalom (MARCSIK, 1971), Hódmezővásárhely—Kotacpart (APOR—NAGY, 1940), Kiskőrös, Szentés—Teés (BARTUCZ, 1966), Palotabozsok

(NEMESKÉRI, 1956), Szentes—Nagyhegy (NEMESKÉRI, 1956), Tiszapolgár—Basatanya (B. KUTZIÁN, 1963; NEMESKÉRI, 1961), Zengővárkony (NEMESKÉRI, 1961; BARTUCZ, 1966).

With respect to the Copper Age, two other comprehensive works are known (NEMESKÉRI, 1956, 1961) in which the author's conclusions were drawn on the basis of the anthropological material of several findspots (Ajka, Alsónémedi, Bodrogkeresztúr, Budakalász, Hajdúdorog, Jászberény—Borsóhalom, Jászládány, Kiskőrös, Kistóke, Konyár, Lebő, Pécel, Pusztaitvánháza, Paszab, Szerencs—Hajdúréti, Tiszapolgár—Basatanya). The material of four cemeteries (Alsónémedi, Budapest—Andor street, Palotabozsok, Szentes—Nagyhegy) were used by TÓTH (1970, 1971, 1972, 1973), as the amalgamated groups of the Baden culture, for analysing the morphogenetic trends.

From among the several finds ascribed to the Bronze Age, scientific evaluation took place only in comparatively few cases. Sites made known so far from the anthropological point of view are: Bag, Kelebia, Üllő (LIPTÁK, 1957), Battonya (FARKAS—LIPTÁK, 1968), the trepanned finds from Deszk—F, Füzesabony, Szeged—János-szállás, Szőreg—C (BARTUCZ, 1966), Pitvaros (FARKAS, 1971), Tápé (FARKAS, 1970; FARKAS—LIPTÁK, 1971, 1971a, 1975; LENGYEL, 1975), Tiszafüred (TÓTH, 1972, 1973).

Also included here are: the comprehensive work of BARTUCZ (1938), the papers dealing with the problem of gracilization (TÓTH, 1968, 1970, 1971, 1972), as well as the publications treating the Bronze Age taxonomy (LIPTÁK, 1957, 1962). The palaeodemographic problems of the Bronze Age are treated in a comprehensive monograph (NEMESKÉRI, 1970). The major problems of prehistory in Hungary (NEMESKÉRI, 1961) are similarly treated.

Considerable prehistoric find-groups in Northern Yugoslavia have also been published. These are: the Copper-Age finds at Nosza-Gyöngypart (FARKAS, 1973), the skeletons from the important Bronze-Age cemetery at Mokrin (FARKAS—LIPTÁK, 1971b; LENGYEL, 1972, 1974, 1974a, 1975; LENGYEL—FARKAS, 1972); the material of the neolithic site Vajška-Baba Sivačka (FARKAS, 1976).

Finally, have been published papers dealing with the burial-rite and the palaeopathological aspects of prehistory in Hungary (FARKAS, 1976a; FARKAS—MARCSIK, 1975), as well as the anthropological evaluation of the Copper-Age cemetery at Magyarhomoróg (FARKAS, 1976b).

All these investigations are, however, very far from exhausting all the possibilities, and the skeletons of several findspots, among them even major series, remain unknown.

It is regrettable that the Bronze-Age anthropological finds excavated by Ferenc Móra in the nineteen-twenties and thirties have not been published to this day. In the Department of Anthropology of the University in Szeged a great many prehistoric finds are stored and have not been made known so far.

We were induced by these facts about ten years ago, to begin studying the prehistoric skeletons from the southern part of the Great Hungarian Plain. Our aim has been to evaluate all the prehistoric palaeoanthropological material of the geographical area bordered by the rivers Tisza—Kőrös—Maros—Aranka and uncovered authentically.

Material investigated

In the course of the work, the material of the following sites — primarily in the southern part of the Great Hungarian Plain and in Northern Yugoslavia — were considered (in brackets we give the identity number of the findspot in the Tables 7—9):

1. From the Neolithic Age (b. o. e. 4000—2500)

A) Kőrös group (b. o. e. 4000—3200): Deszk—1 oil-well (1.1), Endrőd (1.2), Hódmezővásárhely—Bodzáspart (1.3), Hódmezővásárhely—Kopáncs Kovács farmstead (1.4), Hódmezővásárhely—Kopáncs Zsoldos farmstead (1.5), Hódmezővásárhely—Kotacpart Vata farmstead (1.6), Maroslele—Pana (1.7).

B) Tisza civilization (b. o. e. 2900—2500): Békés—Povádzug (1.8), Hódmezővásárhely—Gorzsa Czukor major (1.9), Hódmezővásárhely—Kökénydomb Kapocsi farmstead (1.10), Hódmezővásárhely—Kökénydomb Vörös farmstead (1.11), Nádudvar—Farkaslőr (1.12), Vésztő—Mágori halom (hill) (1.13).

C) Neolithic findspots not described in detail: Ada—Mohol (Northern Yugoslavia, 1.14), Békésszarvas—Szappanoszi szőlők (vineyards) (1.15), Csóka—Kremenyák (N. Yug., 1.16), Hódmezővásárhely—Kökénydomb Kovács farmstead (1.17), Lebő (1.18), Megyesbodzás—Dózsa agricultural co-operative, Mogyorós, Ószentiván VIII (1.19).

2. From the Copper Age (b. o. e. 2400—2000)

A) Tiszapolgár civilization (b. o. e. 2400—2300): Deszk-A (2.1), Deszk-B (2.2), Hódmezővásárhely—Kotacpart Vata farmstead (2.3—2.4), Hódmezővásárhely—Népkert (2.5), Hódmezővásárhely—Szakálhát (2.6), Lebő-A (2.7), Ószentiván VIII (2.8).

B) Bodrogkeresztúr civilization (b. o. e. 2200—2100): Maroslele (2.9), Magyarhomoróg—Könyadomb (2.10), Magyartés (2.11), Nosza-Gyöngypart (N. Yug., 2.12), Szentés—Kistőke Szegi farmstead (2.13), Szentés—Teés (2.14), Vajška—Baba Sivačka (N. Yug., 2.15), Zalota—Bökény crossing-place (2.16).

C) Pécel civilization (b. o. e. 2100—2000): Baja—György Dózsa street 233 (2.17), Hódmezővásárhely—Bodzáspart Pap farmstead (2.18), Orosháza—Bónum „Red Star“ agricultural co-operative (2.19).

3. From the Bronze Age (b. o. e. 2000—1200):

A) From the early Bronze Age (b. o. e. 2000—1800): Battonya—„Red October“ agricultural co-operative (3.1), Deszk-A (3.2), Hódmezővásárhely—Kökénydomb Szabó farmstead (3.3), Mokrin—Lalina humka (N. Yug., 3.4), Óbéba (N. Yug., 3.5), Ószentiván III, IV, and other sites (3.6—3.8), Pitvaros (3.9), Rőszke (3.10), Szolnok—Rákóczi-falva Kastélydomb (3.11), Szőreg-C (3.12), Szőreg—Pálffy brick-works (3.13), Törökkanizsa—Halászká holms (N. Yug., 3.14).

B) From the middle Bronze Age (b. o. e. 1800—1350): Deszk-A (3.15), Deszk-F (3.16), Hódmezővásárhely—Kopáncs Szabó farmstead (3.17), Hódmezővásárhely—Lelik farmstead (3.18), Kelebia (3.19), Szolnok—Rákóczi-falva Kastély-

domb (3.20), Szőreg-C (3.21), Tiszafüred-Fertői halom (hill) (3.22), Tiszafüred—Majoros halom (hill) (3.23), Úllő—Lőb puszta (steppe) (3.24).

Late phase of the middle Bronze Age: Deszk-A (3.25), Deszk-F (3.26), Hódmezővásárhely—Czukur major (3.27), Szőreg-C (3.28), Tiszafüred—Majoros halom (hill) (3.29).

C) From the late Bronze Age (b. o. e. 1350—1200): Bag (3.30), Szolnok—Rákóczi-falva Kastélydomb (3.31), Tápe—Szentégláégető (coalbrick-works) (3.32).

D) Bronze Age finds, not classified into phases: Hódmezővásárhely—State farm (3.33), Hódmezővásárhely—Kökénydomb Szabó farmstead (3.34), Katymár—Prispa (3.35), Szolnok—Rákóczi-falva Kastélydomb (3.36), Szolnok—Water Management (3.37), Szőreg-C (3.38).

A part of these findspots is indicated in Figure 1.



Fig. 1.

Methods of investigation

The comparison of palaeoanthropological finds is, even in the case of a detailed evaluation, very much encumbered in that different methods have been applied by the individual authors. In evaluating the finds from the Southern Great Hungarian Plain, we were striving — for the sake

of biological reconstruction and taking into consideration the possibilities at our disposal — to apply all the methods of investigation that were suitable for elucidating the many facets of the find material. So we used the following methods:

— In establishing sex (sexus), we observed in part some morphological characters (MARTIN—SALLER, 1957—1966; NEMESKÉRI—HARSÁNYI, 1958), evaluated these individually on the basis of the five-grade scale (HARSÁNYI—FÖLDES, 1968), and established the sexuality index. In part — but not in the case of every findspot — the citrate content determined by chemical analysis (LENGYEL—NEMESKÉRI, 1963) was decisive. The reliability of the morphological characters determined was checked by comparing the archaeological and chemical determinations, carried out earlier on the same material (Mokrin), to each other (LENGYEL—FARKAS, 1972). All three determinations coincided 92 per cent of the time.

— For establishing the age at death, we were partly left to using traditional methods (MARTIN—SALLER, 1957—1966) owing to the bad state of preservation of the material. But the methodology serving for a more exact morphological determination (NEMESKÉRI—HARSÁNYI—ACSÁDI, 1960) and the results of the osteochemical investigations (LENGYEL, 1972), were also taken into consideration.

— The metric analysis was performed according to MARTIN's technique. In classifying the characteristics, the arrangement of Hug, MARTIN, and SALLER was taken as our basis. The stature was calculated by the method of BREITINGER and BACH (BREITINGER 1938; BACH 1965). In establishing the morphological features, MARTIN's prescriptions were used.

— In the taxonomical analysis we have depended on LIPTÁK's works. We had earlier established some „norm values“ for the Europoids (FARKAS, 1972, Tables 1 to 6), on the basis of LIPTÁK's publications and, later on, we compared our data to these.

In judging the relative frequency of the single taxonomical categories according to archaeological periods, the dispersion of the relative frequency was taken into consideration. The lower limit of that was determined by the following formula:

$$p'_1 = \frac{p' + \frac{a^2}{2n} - \frac{a}{n} \cdot \sqrt{p'(1-p') + \frac{a^2}{4n}}}{1 + \frac{a^2}{n}}$$

while its upper limit was reckoned by the following formula:

$$p'_2 = \frac{p' + \frac{a^2}{2n} + \frac{a}{n} \cdot \sqrt{p'(1-p') + \frac{a^2}{4n}}}{1 + \frac{a^2}{n}}$$

where p' is the (empirical) relative frequency calculated from the sample, n is the number of elements of the sample, a is the Table value corresponding to reliability level 95 per cent.

— The biochemical and serological characteristics of bones were taken from IMRE LENGYEL (LENGYEL, 1972, 1975).

— In explaining anatomical variations and palaeopathological cases, we have taken for our basis some analogies described primarily after the pattern of BROTWELL (1959), FINNEGAN (1973, 1973a), MARTIN—SALLER (1957—1966), REGÖLY—MÉREI (1962), NATHAN—HAAS (1966) and others.

— In the biometric evaluation we made use of the methods applied to the anthropological problems. The parameters were calculated with a computing machine of type R—40.

— In the palaeodemographic evaluation we leaned on the works of ANGEL (1969), and NEMESKÉRI (1970).

— In classifying the palaeoanthropological finds into archaeological periods, we have studied in addition to the original descriptions, the above-mentioned results of BÓNA, KALICZ, TROGMAYER, and B. KUTZIÁN.

— The coincidence between the mode of interment (right- or left-side one) and the result of the anthropological sex-determination was investigated with a 2×2 field contingency table, and a close connection was established.

Before examining the material of finds, its authenticity was checked in every case. And then, after the investigation was carried out by the methods mentioned above, we compared our data, with the results of foreign publications. Our conclusions were based on the results of the above-mentioned procedures.

Results

1. We studied 53 out of 128 neolithic-grave finds originating from the area of the southern Great Hungarian Plain, 117 out of the 261 graves ascribed to the Copper Age, as well as 1122 skeletons out of the finds of 2303 Bronze-Age graves in this investigation. Altogether 1292 finds of 2692 excavated graves were studied (Tables 7—9).

The number of findspots in the archaeological periods is as follows:

21 neolithic findspots (7 of the Kőrös group, 6 of the Tisza civilization, 8 neolithic findspots, not classified into phases);

20 findspots from the Copper Age (8 of the Tiszapolgár civilization, 8 of the Bodrogheresztúr civilization, 3 of the Pécel civilization, 1 findspot, not classified into phases, of the Copper Age);

38 findspots from the Bronze Age (14 findspots of the early, 10 of the middle, 7 of the late Bronze Age, 1 tumulus, 6 Bronze Age findspots, not classified into phases).

In Hungary this was the first case of detailed anthropological observations on such a great number of skeletal materials from prehistory. This was supplemented by finds already published that don't belong in the strict sense of the word to the area of the southern Great Hungarian Plain and were drawn into the research in the course of comparison.

2. From the Neolithic Age 41.4 per cent, from the Copper Age 44.8 per cent, from the Bronze Age 48.7 per cent of the finds excavated could be studied (Table 10).

Only the skeletons of every second grave were practically rescued or — owing to the fragmentary preservation of the material rescued — only every second find was suitable for more detailed analysis. One of the basic preconditions of anthropological research of prehistory is to have a satisfying quantity of investigatable material at our disposal. It is therefore desirable in the future that during the excavations stronger stress be laid upon rescuing the finds.

3. For establishing the distribution according to sex and the age at death, there were 431 male, 415 female, and 314 infantile skeletons available for us (Tables 7—10).

The above numbers prove that the non-rescued finds came primarily from among the skeletons of children. This fact played a decisive part in the palaeodemographical evaluation. While from among the finds of the southern Great Hungarian Plain 9.4 per cent of the finds belong to the age-groups *Infantia* I—II, in the finds of similar period from the Ukraine this group appears with 67.1 per cent (KONDUKTOROVA, 1973), and among the finds from Bulgaria infantile skeletons are not even mentioned (BOEV, 1972).

Even if we determined the death age of finds exactly and with absolute certainty, our palaeodemographical conclusions would nonetheless be unrealistic, at least concerning the average age.

Moreover, it is striking that the number of those reaching their sixtieth year was quite low in the Neolithic Age.

In the Copper Age, the number of senile and adult ages increased. It is possible that this is but a sham result caused by the difference in the size of series.

In the Bronze Age, those between 0—14 years of age are represented in a cca 8 per cent higher ratio.

The palaeodemographical problems of the Middle-Danube basin were treated by NEMESKÉRI (1970). He established that the life expectancy increased from the Neolithic to the Copper Age, and after that it decreased. It was, however, noted, that his data were to be accepted with some reservation. We agree with him that several conditions ought to be fulfilled for enabling us to thoroughly reveal the pattern. In Hungary the major series necessary for this purpose are only available from the Bronze Age while the Neolithic Age is only represented by a very modest find material. Consequently, we want to give information in Table 11 on the connections between death ages and archaeological periods only on the basis of larger age groups.

4. As we have dealt with the problem of the archaeological and anthropological sex-determination in detail (FARKAS, 1976), here we only want to call attention to some of the more important relationships.

In the Neolithic Age no relation can be proved between the burial rite and sex.

In the Copper Age, in the cemeteries investigated, males were more often buried on their right sides, and females more often on their left sides. This burial custom has correlation coefficient $r=0.691$ calculated for the entire Copper Age. In the early Copper Age, the correlation of the two phenomena ($r=0.658$) is weaker than in the middle Copper Age ($r=0.694$).

In the early period of the Bronze Age, the correlation is still stronger ($r=0.740$). At that time, however, as opposed to the Copper Age, men were buried on their left, and females on their right sides. This may suggest the appearance of a new ethnic group.

In the middle Bronze Age the correlation between the two factors is already loose ($r=0.354$, and for the people of the tumulus civilization it is very loose ($r=-0.075$). That is to say, in case of the latter ones, the sex of skeleton is no longer determined by the side on which it lies in the grave.

The correlation between the two factors increased from the Neolithic Age through the early Bronze Age. Then it decreased, and in the late Bronze Age it was extremely weak.

5. According to the analysis of arithmetic means, every prehistoric phase is characterized, in the case of males, by the medium-long, narrow and medium-high cranium, the medium-high and orthognathous splanchnocranium (Table 12). The upper face is medium-high, the nasal cavity is medium-high, the palate is medium-long and mesen.

According to the indices, the upper face is narrow in the Neolithic and Bronze Ages. In some phases of the Bronze Age it is mesen. The orbit is high (hypsiconch) in the Neolithic Age. In all the other periods it is medium-high (mesoconch). The neurocranium is dolichocranic except for the middle Bronze Age when it is mesocranic. Brachycephalism, on the basis of the arithmetic mean, is not characteristic of any period and can be found in the whole series only 13 per cent of the time, and it occurs very rarely in the Copper Age.

The stature in the Neolithic Age is large-medium, after that it becomes shorter (medium). The large-medium stature is characteristic of the early Bronze Age, too.

It seems that in the late Bronze Age we have to reckon with the inflow of a dolichocephalic male population with larger stature.

Females have, in all the archaeological periods, a broad front, their face is medium-high, leptoprosopé, the orbit is narrow, mesoconch, the nose is chamaerrhine,

the palate is narrow (Table 13). The cranium is, except for the middle Bronze Age, high.

The other features of women in the different periods are much more varied than those of men. The stature is, except for the late Bronze Age, tall or large-medium.

6. On the basis of the taxonomical analysis (354 finds), we have established for the various periods the following:

In the Neolithic Age, the taxonomical features of males and females are different. Among males primarily the Nordoids, among females the Mediterraneans occur. Brachycephalic ones have not been found among either sex. Among the Mediterraneans there are more Atlanto-Mediterraneans than gracile ones. But further finds are absolutely needed for describing the taxonomical picture of the Neolithic Age.

In the Copper Age, in case of males the ratio of Nordoids decreased. The frequency of Mediterraneans and Cromagnoids increased. Compared with the Neolithic Age, the female variability greatly decreased.

The brachycephalic individuals occurred in the Copper Age, in the period of the Tiszapolgár civilization for males, and in the Bodrogheresztúr civilization for females, but, as compared with the other taxons, in a significant number. In both sexes the ratio of the gracile Mediterranean and the Atlanto-Mediterranean variants became balanced.

In the Bronze Age, both among males and females, the Mediterranean group occurs the most frequently, but with decreasing importance. The main reason is primarily the numerical growth of Nordoids, Cromagnoids, and brachycephalic ones. Among males, the most frequent variant is the northern one, among females the Atlanto-Mediterranean. Among the Mediterraneans, in males the gracile, and in females the Atlanto-Mediterranean variants are more frequent. Among the brachycephalic ones, the Alpine race is comparatively more frequent.

Within the Bronze Age, the following is found among both males and females. In the early Bronze Age mainly the Nordoids prevail. In the middle Bronze Age and the late Bronze Age the Mediterranean groups dominate. Among both sexes the brachycephalic ones primarily appear in the early Bronze Age.

The taxonomical variants in the prehistory of the southern Great Hungarian Plain may be followed by other methods, as well. As is known, the transformation of the splanchno- and neurocrania was investigated by Debetz, by means of the praeauricular faciocerebral index. The change of this index was observed by Tóth on the material of the Carpathian basin (TÓTH, 1970, 1971, 1972, 1973). In the case of the finds of the tumulus cemetery at Tápió the value of the index is lower than in the case of the early Bronze Age material. That enables us to draw some inferences concerning the direction of migration.

7. In the case of the palaeopathological evaluation there emerges, unfortunately, the same problem as in drawing the palaeodemographical conclusions: it would be difficult to give the absolute frequency of a given anomaly or anatomical variation because of the incompleteness of the cemetery excavations.

The palaeopathological relationships of the prehistoric series will be mentioned by us in detail (FARKAS—MARCSIK, 1975); here we are only calling attention to a few significant facts.

In the case of the prehistoric series examined, a wide range of anatomical variations and congenital anomalies may be observed. In the case of the finds of the tumu-

lus civilization at Tápé only very few deformations can be observed. Among the early Bronze Age crania at Mokrin, however, the caries frequency was high.

In several cemeteries a large number of trepanned cases were found (Szőreg, Mokrin, Teés), by reason of which we have supposed the functioning of a much experienced „trepanation centre“ in the Maros region, the members of which transferred their experiences to one another, from generation to generation.

8. According to the present-day archaeological approach, in the Neolithic Age the Carpathian basin was occupied by a new population coming probably from the direction of the Balkans (from south or south-east) and leading to an agricultural way of life. It is not impossible, either, that the mesolithic population living here also participated in the formation of the new population (KALICZ, 1970; BÓNA, 1972).

The verification of this conjecture was carried out on the basis of the anthropological material at our disposal. The results of the analysis performed by ANGEL, BOEV, BUNAK, CAPPRIERI, KNUSSMANN, KONDUKTOROVA, NECRASOV, and SCHWIDETZKY were taken into consideration as comparative data. These deal with Asia Minor, the Balkan Peninsula, Central-, Northern-, and South-West Europe, and to the whole of Europe.

On the basis of all these, we were led to the conclusion that the peopling of the Carpathian basin in the Neolithic Age from southern or south-eastern direction (and possibly from both) can be supported with anthropological data, and even a migration from the east cannot be excluded. At the same time, a migration from the north-east (NEMESKÉRI, 1944) would demand, in our opinion, further confirmation. These conclusions of ours are confirmed largely by the results of SCHWIDETZKY (1967, 1967a, 1967b, 1967c) who found great similarity between the finds from Greece, Yugoslavia (Vinča), and Bulgaria, and established that in the Neolithic Age in the southern part of Europe a uniform population complex came into being. The data from Hungary were omitted from the investigation obviously for want of being published. The investigations showed some taxonomical similarity to the populations of the mentioned areas in the Neolithic Age.

9. The origin of the Copper Age civilization in the Carpathian basin is traced back by archaeologists to the Tisza civilization, assuming a migration from the south (KALICZ, 1970; BÓNA, 1972).

To investigate this supposition, we used, apart from the material concerning the southern Great Hungarian Plain, the data of CAPPRIERI (1969, 1970, 1970a), BOEV (1972), KONDUKTOROVA (1973), NECRASOV (1965) and established, on the basis of these, the following:

The finds of the southern Great Hungarian Plain are unequivocally favourable to the supposition that the Copper Age population is of southern origin. That is also confirmed by the approximately 49 per cent frequency of the Mediterraneans. The percentage (17 p.c.) of Cromagnoids did not change with respect to the Neolithic Age. But it is not excluded by the find from Csongrád-Kettőshalom (MARCSIK, 1974), either, that the Copper Age people of this type got into the Carpathian basin from the east. In that period the brachycephalic elements are also represented in the Alpine race (Kotacpart, Kistőke). It is exactly this that supports the supposition that the effect of the Transdanubian Balaton group may have extended over the southern Great Hungarian Plain, too.

Concerning the Pécel civilization we cannot give, because of lack of finds, any additional data. It would also be difficult, in default of anthropological data, to take

part in the question of how the Balaton civilization was related to the Cucuteni – Tripolje civilization (BÓNA, 1972). TÓTH, in one of his publications (1970), calls attention to the fact that he thought the discovered some morphological similarity between the Baden (Pécel) civilization in Hungary and the Tripolje series.

The archaeological observation that the burial rite became more consequential in this period (BÓNA, 1972), can be proved with anthropological data unambiguously.

10. Archaeologists suppose an immigration from the south and east, and in the case of the tumulus civilization a western origin (BÓNA, 1972; TROGMAYER, 1975) in the Bronze Age.

The data from the southern Great Hungarian Plain were compared to the results of TÓTH, NECRASOV, CRISTESCU, BOEV, STROUHAL, JELINEK, EHGARTHNER, MISZKIEWICZ (TÓTH, 1970, 1971, 1972; NECRASOV—CRISTESCU, 1965; BOEV, 1972; STROUHAL, 1964; JELINEK, 1965; EHGARTHNER, 1959; MISZKIEWICZ, 1972).

Concerning the Bronze Age of the southern Great Hungarian Plain, it can be established that the Carpathian basin became filled with people from southern and eastern directions in the early Bronze Age. That is verified with anthropological data as well. At the same time, it seems to us that the people arriving from the east may have had greater importance which is rendered probable by the increase in the ratio of Nordoids and Cromagnoids and the decrease in that of the Mediterraneans. In addition, the relationship between the Pitvaros group and the Nagyrév civilization is to be supposed as well. This latter establishment is reinforced by the fact that in the archaeological material of the so-called Pitvaros group of the early Bronze Age there was a pot belonging to the Nagyrév civilization as grave-furniture in the grave of a brachycephalic female, who was different even in this taxonomical respect (FARKAS, 1971).

The anthropological data from the southern Great Hungarian Plain are in accord with the archaeological observations of the middle Bronze Age. The Balcanic effect can be considered verified. From the late phase of the middle Bronze Age we have but few finds from the southern Great Hungarian Plain. Therefore, we cannot prove or disprove the migration process supposed.

The western origin of the tumulus civilization does not seem to be verified on the basis of the material of the cemetery at Tápé as the frequency of Mediterraneans is 60 per cent. At the same time, the immigration from the west is confirmed by the anthropological observations in Slovakia, Austria, and Poland. The antagonism between western origin and taxonomical distribution is explained by the fact that only about 10 per cent of the 600 finds could be analysed by a taxonomical method. The percentile distribution is, in this case, misleading (the dispersion of the relative frequency is large, Table 14). At the same time, we should like to refer again to the fact that the value of the preauricular cerebral index does not fit in well with the finds from Tápé. This supports, in an indirect way, the deviation from the earlier, southern direction of migration in the case of the tumulus civilization.

Table 1. Characteristics of Euroid Males.

Characteristic	crA $n^+ = 23 - 33$	crB $n = 3 - 12$
1. Cranial contour Cranial capacity	Ov.-Ell. 1419 ± 120 Euencephalic	Pent.-Spher. 1495 ± 169 Aristencephalic
2. First cran. dim. 8th cran. dim. 17th cran. dim.	186 ± 6 medium 142 ± 6 medium 132 ± 6 medium	179 ± 8 short 147 ± 6 medium 134 ± 8 medium
3. 8:1 index 17:1 index 17:8 index	76 ± 2 mesocranic 71 ± 3 orthocranic 93 ± 5 metriocranic	92 ± 4 brachycranic 74 ± 4 orthocranic 91 tapeinocranic
4. 9:8 index Frontal shape Glabella	70 ± 4 eurymetopic moder. prognathic 3—4	68 ± 3 metriometopic 2
5. 47:45 index 48:45 index 72nd cran. dim.	81 ± 4 euryprosop. 49 ± 3 euryen 85 ± 4 orthognath.	82 ± 4 euryprosop. 48 ± 2 euryen 86 ± 4 orthognathous
6. 52:51 index Orbital shape	78 ± 6 mesoconch angular, oblong	77 ± 9 mesoconch angular, oblong
7. 54:55 index Nasal shape	53 ± 5 chamaerrhine protruding, straight or curved	56 ± 4 chamaerrhine protruding, concave
8. Fossa canina Branch of mandible	4—6 low	4 high, medium
9. Spec. type-char.	square face gonion projecting	square face gonion projecting
10. Stature Skeleton	168 ± 4 big medium robust	162 ± 2 small medium robust
Prot. occ. ext. Spina nas. ant. Alv. progn.	2—1 2—3 1—2	0 2 2

n^+ = in the Tables the case-number (n) is different according to characters, e. g. for the taxon crA it ranges between 23 and 33.

Table 2. Characteristics of Europid Males.

pn n = 5-13	n n = 39-78	m n = 29-49
Ov.-Ell. 1405 ± 92 Euencephalic	Ov.-Ell. 1477 ± 104 Aristencephalic	Pent.-Ov.-Ell. 1319 ± 89 Euencephalic
193 ± 7 long 139 ± 4 narrow 134 ± 6 medium	190 ± 6 long 141 ± 5 medium 136 ± 6 medium	181 ± 6 medium 134 ± 5 narrow 131 ± 5 medium
73 ± 4 dolichocranic 71 orthocranic 96 ± 5 metriocranic	74 ± 3 dolichocranic 72 ± 3 orthocranic 97 ± 5 metriocranic	74 ± 3 dolichocranic 73 ± 3 orthocranic 97 ± 5 metriocranic
70 ± 2 eurymetopic 5	70 ± 3 eurymetopic arcuate, modestly protruding 3	70 ± 4 eurymetopic arcuate 1-3
96 ± 7 h. leptopr. 57 ± 5 lepten 86 ± 3 orthognathous	92 ± 4 leptoprosop 55 ± 3 lepten 87 ± 3 orthognath.	93 ± 5 leptoprosop 55 ± 3 lepten 85 ± 4 orthognathous
82 ± 7 mesoconch	84 ± 7 mesoconch angular	84 ± 6 mesoconch round
48 ± 4 mesorrhine	48 ± 4 mesorrhine straight, convex	49 ± 5 mesorrhine straight
2 or 4	2-3	2-3 medium
sharp, gerontomorphous	big abs. measurements	gracile, small abs. measurement
169 ± 3 big medium	169 ± 5 big medium robust	161 ± 5 small medium gracile
3 2-4 1-3	1-2 2-3 1-2	0-1 4 1-2

Table 3. Characteristics of Europic Males.

am n = 7—12	a n = 2—6	p n = 12—18
Pent. 1377 ± 120 Euencephalic	Pent.-Ov. 1419 ± 95 Euencephalic	Pent.-Sphen.-Spher. 1500 ± 111 Aristencephalic
185 ± 3 medium 135 ± 4 narrow 133 ± 4 medium	176 ± 6 short 144 ± 3 medium 133 ± 4 medium	178 ± 7 short 151 ± 6 broad 136 ± 6 medium
73 ± 2 dolichocranic 72 ± 3 orthocranic 99 ± 4 acrocranic	82 ± 3 brachycranic 75 ± 2 hypsicranic 92 ± 3 metriocranic	85 ± 5 h. brachycranic 76 ± 3 hypsicranic 91 ± 6 tapeinocranic
71 ± 2 eurymetopic 2—3	66 ± 3 metriometop. arcuate 2	65 ± 2 stenometopic steep 2—3
92 ± 5 leptoprosopie 56 ± 4 lepten 86 ± 3 orthognathous	88 ± 3 mesoprosopie 51 ± 2 mesen 86 ± 3 orthognath.	88 ± 3 mesoprosopie 53 ± 2 mesen 85 ± 4 orthognathous
87 ± 5 hypsiconch	86 ± 5 hypsiconch round	85 ± 7 hypsiconch
46 ± 3 leptorrhine	50 ± 4 mesorrhine straight, short	46 ± 3 leptorrhine modestly protruding, straight or curved
2—3	2 medium	1—4
extremely high, narrow face	curvoccipitalia	lambdoid region is flat, forehead steep, curvoccipitalia
168 ± 4 big medium	162 ± 7 small medium, medium	167 ± 3 big medium
0—2 4 1—3	0 or 2 3 1	1—2 3 1

Table 4. Characteristics of Europid Females.

crA n=9—16	crB n=9—15	n n=26—65
Ov.-Ell.-Sphen. 1342±81 Aristencephalic	Ov.-Sphen. 1280±132 Euencephalic	Ov.-Pent. 1300±98 Euencephalic
180±5 long 137±3 medium 129±6 medium	169±8 short 140±6 medium 125±5 medium	181±5 long 135±4 medium 129±6 medium
76±2 mesocranic 72±3 orthocranic 95±5 metriocranic	83±2 brachyranic 73±3 orthocranic 89±4 tapeinocr.	74±3 dolichocranic 72±3 orthocranic 96±5 metriocranic
70±3 eurymetopic modestly protruding 1—2	68±3 metriometop. 1—2	70±3 eurymetopic arcuate 1—2
80±5 euryprosope 48±3 euryen 83±5 mesognathous	84±5 euryprosope 50±3 mesen 84±4 mesognath.	91±4 leptoprosope 54±3 mesen 85±4 orthognathous
82±6 mesoconch angular, oblong	83±6 mesoconch modestly angular	85±5 hypsiconch round
51±6 chamaerrhine straight, convex	51±4 chamaerrh. straight, concave	48±4 mesorrhine straight, convex
2—3 low	2—3 high	2—4 high
square face, gonion projecting	square face, gonion projecting	
156±3 big medium medium	151±3 small medium medium	157±3 big medium medium
1—3 2—3 2	0—1 2 1—3	0—1 1—3 1—3

Table 5. Characteristics of Europid Females.

m n = 29—46	am n = 7—9
Pent.-Ov. 1204 ± 72 Euencephalic	Ov.-Pent. 1326 ± 117 Aristencephalic
175 ± 4 medium 132 ± 5 narrow 126 ± 4 medium.	180 ± 7 long 134 ± 4 narrow 130 ± 5 medium
75 ± 3 mesocranic 72 ± 2 orthocranic 96 ± 4 metriocranic	75 ± 4 mesocranic 72 ± 2 orthocranic 97 ± 4 metriocranic
70 ± 3 eurymetopic arcuate 1—2	71 ± 3 eurymetopic 1—2
90 ± 4 leptoprosope 55 ± 3 lepten 85 ± 3 orthognathous	95 ± 6 h. leptoprosope 58 ± 4 lepten 84 ± 2 mesognathous
86 ± 5 hypsiconch round	91 ± 9 hypsiconch
49 ± 5 mesorrhine	47 ± 6 mesorrhine
1—4	2—3
gracile	
152 ± 4 small medium gracile	159 ± 2 tall
0—1 1—3 2—3	0—1 2 2—3

Table 6. Characteristics of Euroid Females.

a n = 4—10	p n = 4—14
Sphen.-Spher.-Ov. 1325 ± 108 Aristencephalic	Pent.-Sphen. 1280 ± 114 Euencephalic
172 ± 6 medium 142 ± 5 medium 127 ± 5 medium	171 ± 7 medium 144 ± 8 medium 130 ± 7 medium
83 ± 2 brachycranial 74 ± 3 orthocranial 89 ± 3 tapeinocranial	84 ± 3 brachycranial 77 ± 5 hypsicranial 93 ± 6 metriocranial
66 ± 3 metriometopic arcuate 1	65 ± 4 stenometopic 1—2
89 mesoprosop 52 ± 1 mesen 86 ± 4 orthognathous	89 ± 3 mesoprosop 54 ± 2 mesen 88 ± 3 orthognathous
86 ± 3 hypsiconch round	84 ± 5 mesoconch
50 ± 4 mesorrhine	49 ± 4 mesorrhine
2—3 medium	
curvoccipitalia	
151 ± 2 small medium medium	155 ± 3 medium
0—1 2—3 2	0 4 2

Table 7. Summary of the Neolithic Age findspots taken into consideration.

Findspot	Excavator, year of excavation	Archaeological age	Grave excavated					Find examined				
			M	F	Ch.	?	Tog.	M	F	Ch.	?	Tog.
4.1.1.	TROGMAYER, 1968	Körös group	1	1	—	—	2	—	2	—	—	2
4.1.2.	MÓRA, 1930	Körös group	1	—	—	—	3	1	—	—	—	1
4.1.3.	BANNER, 1939	Körös group	—	—	1	2	3	1	—	—	—	1
4.1.3.	BANNER, 1948	Körös group	1	—	—	6	7	—	—	—	—	—
4.1.4.	BANNER, 1932	Körös group	—	—	2	2	4	—	—	—	—	—
4.1.5.	BANNER, 1931	Körös group	1	2	3	3	9	—	—	—	—	10
4.1.6.	BANNER, 1934	Körös group	2	1	2	6	11	6	4	—	—	5
4.1.7.	TROGMAYER, 1963	Körös group	2	1	1	1	5	2	1	1	1	5
Together:			8	5	9	22	44	10	7	1	1	19
4.1.8.	TROGMAYER, 1958	Tisza civilization	4	2	—	—	7	4	2	—	—	6
4.1.9.	GAZDAPUSZTAL, 1956—57	Tisza civilization	—	—	—	—	9	—	—	—	—	—
4.1.9.	GAZDAPUSZTAL, 1963	Tisza civilization	1	2	1	—	4	1	2	1	—	4
4.1.10.	BANNER, 1928	Tisza civilization	5	4	3	3	15	—	—	—	—	—
4.1.10.	BANNER, 1941	Tisza civilization	—	1	1	—	2	—	1	1	—	2
4.1.10.	BANNER, 1942	Tisza civilization	—	—	1	—	1	—	—	1	—	1
4.1.11.	BANNER, 1941	Tisza civilization	—	1	—	—	1	—	1	—	—	1
4.1.12.	GAZDAPUSZTAL, 1962	Tisza civilization	—	—	2	—	2	—	—	2	—	2
4.1.13.	HEGEDŰS, 1972	Tisza civilization	4	4	5	2	15	4	4	5	—	13
Together:			14	14	13	15	56	9	10	10	—	29
4.1.14.	KRECSMÁRIK, 1926	Neolithic Age	—	—	—	1	1	—	—	—	—	—
4.1.15.	KRECSMÁRIK, 1911	Neolithic Age	1	1	1	2	5	—	—	—	—	—
4.1.16.	GUBITZA, 1904	Neolithic Age	—	—	—	1	1	—	—	—	—	—
4.1.16.	MÓRA, 1907—13	Neolithic Age	—	1	1	7	9	—	—	—	—	—
4.1.17.	BANNER, 1928	Neolithic Age	2	—	2	1	5	—	—	—	—	—
4.1.18.	REIZNER, 1904?	Neolithic Age	—	—	—	3	3	1	—	—	—	1
4.1.19.	Museum of Szeged?	Neolithic Age	1	—	—	—	1	1	—	—	—	1
4.1.19.	KÖREK, 1943	Neolithic Age	—	1	—	—	1	—	1	—	—	1
4.1.19.	B. KUTZIÁN, 1960	Neolithic Age?	—	1	—	—	1	—	1	—	—	1
4.1.19.		Neolithic Age	1	—	—	—	1	1	—	—	—	1
Together:			5	4	4	15	28	3	2	—	—	5
Altogether:			27	23	26	52	128	22	19	11	1	53

Table 8. Summary of the Copper Age findspots taken into consideration.

Findspot	Excavator, year of excavation	Archaeological age	Grave excavated					Find examined				
			M	F	Ch.	?	Tog.	M	F	Ch.	?	Tog.
4.2.1.	MÓRA, 1930—31	Tiszapolgár civ.	2	9	1	1	13	2	3	—	—	5
4.2.2.	MÓRA, 1930—31	Tiszapolgár civ.	7	3	1	3	14	4	3	1	—	8
4.2.3.	PÁRDUCZ—BANNER, 1932—33	Tiszapolgár civ.	10	5	6	5	26	5	5	1	—	11
4.2.4.	BANNER, 1933—34	Tiszapolgár civ.	1	7	6	2	16	2	5	1	—	8
4.2.5.	GAZDAPUSZTAI, 1960, 1963, NAGY K. 1965	Tiszapolgár civ.	1	4	—	1	6	—	2	—	—	2
4.2.6.	BANNER—BÁLINT, 1934	Tiszapolgár civ.	—	1	—	—	1	—	1	—	—	1
4.2.6.	BANNER, 1935	Tiszapolgár civ.	—	1	—	—	1	—	1	—	—	1
4.2.7.	MÓRA, 1928, 1930	Early Copper Age	2	11	2	3	18	2	2	1	—	5
4.2.7.	REIZNER, 1904	Early Copper Age	—	—	—	3	3	—	—	—	—	—
4.2.7.	KÖREK—PÁRDUCZ, 1950	Early Copper Age	5	6	2	1	14	—	—	—	—	—
4.2.7.	TROGMAYER, 1956	Tiszapolgár civ.	2	1	—	—	3	2	—	—	—	2
4.2.8.	TÓTH, 1942	Tiszapolgár civ.	1	1	—	—	2	—	2	—	—	2
4.2.8.	B. KUTZIÁN, 1960	Tiszapolgár civ.	—	1	—	—	1	1	—	—	—	1
Together:			31	50	18	19	118	18	23	4	—	45
4.2.9.	?	Bodrogkeresztúr c.	—	2	—	—	2	—	2	—	—	2
4.2.10.	DIENES—PATAY, 1961—70	Bodrogkeresztúr c.	16	19	2	47	84	18	15	6	9	48
4.2.11.	CSALLÁNY G., 1937	Bodrogkeresztúr c.	1	1	3	1	6	2	—	1	—	3
4.2.12.	Museum of Subotica, 1952—54	Bodrogkeresztúr c.	5	2	—	—	7	5	2	—	—	7
4.2.13.	CSALLÁNY G., 1930	Bodrogkeresztúr c.	7	19	2	—	28	1	1	—	—	2
4.2.14.	?	Bodrogkeresztúr c.	1	1	1	—	3	1	1	—	—	2
4.2.15.	BRUKNER—MEDOVIĆ, 1966—67	Bodrogkeresztúr c.	1	5	—	—	6	1	5	—	—	6
4.2.16.	Museum of Szentes, 1932	Bodrogkeresztúr c.	1	1	—	—	2	—	—	—	—	—
Together:			32	50	8	48	138	28	26	7	9	70
4.2.17.	KŐHEGYI, 1960	Pécel civilization	1	—	—	—	1	1	—	—	—	1
4.2.18.	BANNER, 1939	Pécel civilization	—	—	—	1	1	—	—	—	—	—
4.2.18.	BANNER, 1948	Pécel civilization	—	—	—	1	1	—	—	—	—	—
4.2.19.	OLASZ, 1960	Pécel civilization	—	—	1	1	2	—	—	1	—	1
Together:			1	—	1	3	5	1	—	1	—	2
Altogether:			64	100	27	70	261	47	49	12	9	117

Table 9. Summary of the Bronze Age findspots taken into consideration.

Findspot	Excavator, year of excavation	Archaeological age	Grave excavated					Find examined				
			M	F	Ch.	?	Tog.	M	F	Ch.	?	Tog.
4.3.1.	GAZDAPUSZTAL, 1964-66	Early Bronze Age	11	13	25	10	59	11	13	25	10	59
4.3.2.	MÓRA, 1930-31	Early Bronze Age	3	4	—	—	7	1	—	—	—	1
4.3.3.	BANNER-FOLTINY, 1940	Early Bronze Age	—	—	—	2	2	—	1	—	—	1
4.3.4.	GIRIČ, 1958-69	Early Bronze Age	90	101	95	26	312	77	86	58	16	237
4.3.5.	? 1902	Early Bronze Age	—	—	—	10	10	—	—	—	—	—
4.3.5.	REIZNER-TÖRÖK, 1903	Early Bronze Age	6	7	1	4	18	—	—	—	—	—
4.3.6.	BANNER, 1926-27	Early Bronze Age	1	6	2	5	14	—	—	—	—	—
4.3.6.	BANNER, 1928	Early Bronze Age	9	7	2	1	19	—	—	—	—	—
4.3.6.	BANNER, 1929	Early Bronze Age	1	1	3	—	5	1	1	—	—	2
4.3.7.	BANNER, 1926	Early Bronze Age	—	—	—	3	3	—	—	—	—	—
4.3.8.	KÖREK, 1943	Early Bronze Age	—	—	—	1	1	—	—	—	—	—
4.3.9.	MÓRA, 1926	Early Bronze Age	10	13	1	20	44	6	7	1	—	14
4.3.10.	MÓRA, 1927-28	Early Bronze Age	—	—	—	3	3	1	1	—	—	2
4.3.11.	KAPOSVÁRI, 1957	Early Bronze Age	—	—	—	1	1	—	—	—	—	—
4.3.11.	CSALOG Zs., 1962	Early Bronze Age	—	—	—	9	9	2	—	—	1	3
4.3.12.	MÓRA, 1928-31	Early Bronze Age	21	5	2	6	34	6	9	5	—	20
4.3.13.	? 1902	Early Bronze Age	1	—	—	—	1	1	—	—	—	1
4.3.14.	WAGNER, 1890	Early Bronze Age	—	4	1	—	5	—	—	—	—	—
Together:			153	161	132	101	547	106	118	89	27	340
4.3.15.	MÓRA, 1930-31	Middle Bronze Age	15	14	—	7	36	4	5	—	—	9
4.3.16.	MÓRA, 1932	Middle Bronze Age	28	23	2	15	68	16	10	4	—	30
4.3.18.	BANNER, 1941	Middle Bronze Age	—	1	—	1	2	1	—	—	—	1
4.3.19.	ZALOTAY, 1954	Middle Bronze Age	—	—	—	125	125	1	4	6	—	11
4.3.20.	CSALOG Zs., 1962	Middle Bronze Age	—	—	—	3	3	—	—	—	—	—
4.3.21.	MÓRA, 1928-31	Middle Bronze Age	41	27	4	13	85	24	19	6	—	49
4.3.22.	CSALOG Zs., 1964	Middle Bronze Age	—	—	—	25	25	—	3	—	—	—
4.3.23.	CSALOG Zs., 1961-64, KOVÁCS T., 1966-71	Middle Bronze Age	—	—	—	370	370	—	—	2	—	5
Together:			84	66	6	559	715	46	42	18	—	106

Table 9. (continued).

Findspot	Excavator, year of excavation	Archaeological age	Grave excavated					Find examined				
			M	F	Ch.	?	Tog.	M	F	Ch.	?	Tog.
4.3.25. 4.3.26. 4.3.27. 4.3.28. 4.3.29.	MÓRA, 1930—31 MÓRA, 1932 GAZDAPUSZTAL, 1963 MÓRA, 1928—31 CSALOG Zs., 1961, 1964 KOVÁCS T., 1966—71	Late phase of middle Bronze Age	1 1 — 24 —	— — — 14 —	2 — 1 10 —	3 1 — 11 246	6 2 1 59 246	— 1 — 9 —	— — — 15 —	— — 1 3 —	— — — — —	— 1 1 27 —
Together:			26	14	13	261	314	10	15	4	—	29
4.3.30. 4.3.31. 4.3.32.	MOZSOLICS, 1949 CSALOG Zs., 1962 TROGMAYER, 1960—66	Late Bronze Age	1 2 186	— 2 159	— 9 162	— 50 72	1 63 579	1 2 186	— 2 159	— 9 162	— 20 72	1 33 579
Together:			189	161	171	122	643	189	161	171	92	613
4.3.33. 4.3.34. 4.3.35. 4.3.36. 4.3.37. 4.3.38.	GAZDAPUSZTAL, 1964 BANNER—FOLTINY, 1940 KÓHEGYI, 1960 CSALOG Zs., 1962 Museum of Szolnok? MÓRA, 1928—31	Bronze Age Bronze Age Bronze Age Bronze Age Bronze Age Bronze Age	2 — — 2 1 6	— — — 5 — 5	— — 1 4 — 37	— 4 5 3 — 10	2 4 6 14 1 57	2 — — 2 1 6	— — — 5 — 6	— 1 1 4 — 3	— — — 3 — —	2 1 1 14 1 15
Together:			11	10	41	22	84	11	11	9	3	34
Altogether:			463	412	363	1065	2303	362	347	291	122	1122
Sum of the complete material investigated:			554	535	416	1187	2692	431	415	314	132	1292

Table 10. Summary of the finds investigated according to archaeological ages.

Archaeological Age	Finds investigated									
	No.					Percentage				
	of the finds excavated									
	M	F	Ch.	?	Together	M	F	Ch.	?	Together
<i>Neolithic Age:</i>										
Kőrös group	10	7	1	1	19	?	?	11,1	4,5	43,2
Tisza civilization	9	10	10	—	29	64,3	71,4	76,9	0	51,8
No civilization determined	3	2	—	—	5	60,0	50,0	0	0	17,9
Sum of Neolithic Age:	22	19	11	1	53	81,5	73,9	42,3	1,9	41,4
<i>Copper Age:</i>										
Tiszapolgár civilization	18	23	4	—	45	58,1	46,0	22,2	0	38,1
Bodrogkeresztúr civilization	28	26	7	9	70	87,5	52,0	87,5	18,8	58,8
Pécel civilization	1	—	1	—	2	100,0	0	100,0	0	40,0
Sum of Copper Age:	47	49	12	9	117	76,6	49,0	44,4	12,8	44,8
<i>Bronze Age:</i>										
Early Bronze Age	106	118	89	27	340	69,3	73,3	67,4	26,7	62,2
Middle Bronze Age	46	42	18	—	106	54,8	63,6	?	0	14,8
Late phase of the Middle B. A.	10	15	4	—	29	38,4	?	30,7	0	9,2
Late Bronze Age	189	161	171	92	613	100,0	100,0	100,0	75,4	95,3
No civilization determined	11	11	9	3	34	100,0	?	21,9	13,6	40,5
Sum of Bronze Age:	362	347	291	122	1122	78,2	84,2	80,2	11,5	48,7
Prehistoric Ages altogether:	431	415	314	132	1292	77,8	77,2	75,5	11,1	48,0

Table 11. Distribution of the material investigated according to ages at death, sexes, and archaeological Ages.

Archaeological Age and Sex Age at death		Neolithic Age			Copper Age			Bronze Age			Together		
		M	F	Ch.	M	F	Ch.	M	F	Ch.	M	F	Ch.
Infantia I.	n %	—	—	4 8,7	—	—	—	—	—	76 8,5	—	—	80 7,7
Infantia II	n %	—	—	4 8,7	—	—	7 7,2	—	—	168 18,8	—	—	179 17,2
Juvenile	n %	—	1 2,2	—	12 1,0	2 2,1	2 2,1	12 1,3	6 0,7	34 3,8	13 1,3	9 0,9	36 3,5
Adult	n %	9 19,6	14 30,4	—	10 10,3	27 27,8	—	165 18,4	201 22,5	—	184 17,7	242 23,3	—
Maturus	n %	8 17,4	1 2,2	—	16 16,5	6 6,2	—	103 11,5	73 8,2	—	127 12,2	80 7,7	—
Senium	n %	3 6,5	2 4,3	—	15 15,5	11 11,3	—	28 3,1	29 3,2	—	46 4,4	42 4,1	—
Together:	n %	20 43,5	18 39,1	8 17,4	42 43,3	46 47,4	9 9,3	308 34,4	309 34,5	278 31,1	370 35,6	373 35,9	295 28,4
Altogether:		46			97			895			1038		

Table 12. Parameters of the main characteristics. — Males.

Archaeological Ages Characteristic	I. Neolithic Age		II. Copper Age		III. Bronze Age		Prehistoric Ages together	
	n	\bar{x}	n	\bar{x}	n	\bar{x}	n	\bar{x}
1.	14	180,78	27	178,37	206	177,82	247	178,05
8.	14	135,50	27	132,22	195	134,43	236	134,24
9.	13	92,92	20	93,10	182	93,77	215	93,66
17.	5	136,80	7	133,71	47	132,38	59	132,91
20.	13	115,30	12	113,08	123	113,15	148	113,33
45.	5	115,00	4	112,00	43	122,13	52	120,66
47.	8	112,25	5	109,60	55	110,92	68	110,98
48.	7	67,42	8	61,50	63	66,32	78	65,92
51.	7	38,57	11	37,63	66	38,57	84	38,45
52.	9	31,00	11	31,90	72	32,56	92	32,42
54.	7	26,57	10	25,00	48	24,71	65	24,95
55.	7	47,71	10	48,60	61	48,36	78	48,33
62.	8	44,75	13	42,38	38	42,31	59	42,66
63.	9	37,11	13	35,69	45	36,55	67	36,46
8:1	14	74,93	24	74,01	179	75,04	217	74,92
17:1	5	76,20	7	74,48	47	75,89	59	75,75
17:8	5	102,40	7	102,80	45	97,22	57	98,36
9:8	13	68,62	19	70,73	155	69,52	187	69,58
47:45	4	98,48	2	98,50	35	91,46	41	92,49
48:45	3	59,47	5	58,98	40	54,65	48	55,40
52:51	7	80,04	9	83,12	63	84,36	79	83,84
54:55	6	55,53	8	51,59	41	51,05	55	51,62
63:62	8	84,80	12	83,31	34	87,73	54	86,31
Calc. stature	6	159,38	10	160,52	170	156,06	186	156,41

Table 13. Parameters of the main characteristics. — Females.

Archaeological Ages Characteristic	I. Neolithic Age		II. Copper Age		III. Bronze Age		Prehistoric Ages together	
	n	\bar{x}	n	\bar{x}	n	\bar{x}	n	\bar{x}
1.	13	188,15	24	189,45	200	186,35	237	186,76
8.	15	138,20	26	136,50	191	136,33	232	136,46
9.	16	97,87	21	97,76	181	96,36	218	96,61
17.	4	132,75	8	136,87	42	136,78	54	136,50
20.	8	116,75	11	118,09	139	116,59	158	116,70
45.	2	128,50	7	131,11	51	129,86	60	129,96
47.	5	118,60	9	119,11	69	116,14	83	116,12
48.	6	71,00	12	71,16	72	69,17	90	69,55
51.	7	38,71	13	40,23	82	39,50	102	39,54
52.	7	33,71	13	31,69	93	32,41	113	32,41
54.	6	26,66	14	25,85	60	25,03	80	25,30
55.	7	51,57	12	51,16	75	51,71	94	51,63
62.	9	44,33	16	45,81	48	43,75	73	44,26
63.	9	39,22	15	38,46	60	38,26	84	38,40
8:1	12	74,01	22	73,08	175	73,51	209	73,49
17:1	2	77,24	8	73,66	42	75,08	52	74,94
17:8	8	80,65	8	100,62	42	96,72	58	95,04
9:8	9	72,19	19	71,24	155	70,97	183	70,73
47:45	2	89,50	5	94,90	45	89,72	52	90,21
48:45	2	55,65	7	56,70	45	54,27	54	54,63
52:51	7	87,00	13	79,01	79	82,27	99	82,18
54:55	5	53,18	11	50,50	58	49,84	74	50,16
63:62	7	87,46	13	83,11	45	89,22	65	87,81
Calc. stature	11	169,46	7	165,91	186	165,62	204	165,84

Table 14. Absolute and relative frequency of the taxonomical groups, confidence intervals of the relative frequencies according to archaeological Ages.

Archaeological Ages		Neolithic Age	Copper Age	Bronze Age	Together
Taxonomical groups					
Nordoids	n	15	10	82	107
	%	55,5	28,6	28,1	30,2
	P ₁ —P ₂	37,3—72,2	15,5—44,1	23,3—33,6	25,6—35,1
Cromagnoids	n	3	6	50	59
	%	11,1	17,1	17,1	16,7
	P ₁ —P ₂	4,0—27,8	8,1—32,6	13,3—21,8	13,2—20,8
Mediterraneans	n	9	17	116	142
	%	33,3	48,6	39,7	40,1
	P ₁ —P ₂	18,9—51,8	33,2—64,2	34,3—45,4	35,2—45,2
Brachycrans	n	—	2	44	46
	%	—	5,7	15,1	13,0
	P ₁ —P ₂	—	1,7—18,4	11,3—19,8	11,0—15,7
Sum total:	n	27	35	292	354

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THE TAXONOMIC METHOD IN HUNGARY AND ITS APPLICATION IN THE PALAEOANTHROPOLOGICAL RESEARCH

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Abstract

The author sums up the prehistorical anthropological (paleoanthropological) researches carried out in Hungary with the taxonomical method between 1950 and 1975. The fundamental principle of the method is that *Homo sapiens* is a polytypical species, that is to say it is divided into sub-species (geographical races). In historical times, thus in Hungary particularly in the migration period (the so-called „Völkerwanderung”) and in the age of the Hungarian conquest of this country (century 10), there took place considerable migrations. At the series of the migration period, not only the taxons of the Europid but even some taxons of the Mongolid great race may be demonstrated on the basis of an analysis performed within the series. The simplest verification of the taxonomical method is to establish the taxon mean. In this paper, the development of the taxonomy of Europids and Mongolids, based on their skeletal material, as well as the metric characterization of human races are coming into question.

There are several possibilities for the anthropological (paleoanthropological) investigation of skeletal material originating from authentic excavations. One of these is taxonomical analysis. Its theoretical basis is given by the fact that *Homo sapiens* is not only polymorphic, but also a polytypic species. Hominid evolution took place in the framework of a polytypic species and ramified into some subspecies (geographical races).

In a later period of hominid evolution — which may be called the history of mankind in biological sense — a decisive factor was the migration of human populations. Because of the migration of the more or less isolated geographic races (great-race), the stratification of human populations and their interbreeding here have occurred with increasing frequency a phenomenon that never takes place in animal populations. It should also be noted that, apart from the four great races (Europid, Mongolid, Negrid and Veddo-Australid) some misco-subspecies also developed. The number of these varies according to whether or not the anthropologist that investigates or compares the populations peopling the earth belongs to the lumpers or the splitter type with respect to his work of classification.

During the twenty years between 1950 and 1970 I endeavoured, relying on the works of Hungarian and foreign anthropologists, particularly in connection with the investigation of the skeletal remains originating from the Age of Migration (so-called „Völkerwanderung”) in Hungarian territory (Avars, Hungarians) — to develop a taxonomy on the basis of the skeletal material (cranosystematics), primarily with regard to Europids and Mongolids. The necessity of developing the method was suggested almost imperatively by the Avar-age series because within the same

cemetery, the subpopulations (clans, ethnic groups) representing two great-races (Europids- Mongolids) were not rarely buried beside each other.

The investigations and results have mostly been published in English, German, or French languages, some of which are not easily accessible for the palaeoanthropologists interested. The outlines of the established systematization (taxonomy) was also published repeatedly, but, from the point of view of its practical application, a comprehensive presentation of the results seems to be necessary. In this comprehensive work I am trying to describe the process in the course of which these results were produced. I do not want to give any full details here of further fundamental principles of the taxonomical system. Instead, I refer to the following works (LIPTÁK 1957b, 1959, 1962, 1963b, 1965, 1969). Concerning the classification I remark that in general I speak of human races that I call taxons or sometimes types. In all these cases I think primarily of the skeletal material. As in the anthropological literature the characterizations concerning the living populations predominate I was anxious to keep this in view making my terms parallel with these.

On the basis of investigating the Ostyak crania collected by JÁNOS JANKÓ in Western Siberia in the region of the middle-Ob and the river Yugan (LIPTÁK, 1950), the metrical and morphological characterization of the Uralian (Ugrian) taxon has become possible. On the conquering Magyars of the tenth century the Uralian race can be demonstrated as well (LIPTÁK, 1951). On the skeletal material of the entirely excavated cemetery of nearly 400 graves at Kérpusztá, from the eleventh century (Árpádian Age), it was first possible to carry out a detailed taxonomical analysis with reference to the appropriate comparisons (LIPTÁK, 1953). The taxons are verified as „real“ by the calculated mean values. Concerning the crania of the separate taxons, the characteristic data are given by 9 metrical data, 8 indices and the mean of body height, together with the frequency of the taxon. The selection of morphological characters according to the principle of taxonomical relevance also advance differential diagnosis which cannot be mentioned in this short paper. In the series of Kérpusztá, that has an almost completely Europid character, the following main taxons could be distinguished with adequately high frequencies: In males: Gracile-Mediterranean (its sign is *m*), Cromagnoid-A (*crA*), Cromagnoid-B or Eastern-Europid (*crB*), and the Dinaric element (*d*) (Table 1). The middle-values concerning the Alpine (*a*) and Nordoid-Atlanto-mediterranean (*n*) taxons cannot be considered completely reliable, owing to the low case number. — In females: three races are important owing to their numerical ratio: the Gracile-Mediterranean, the Cromagnoid-B, and the Cromagnoid-A (Table 2).

The Dinaric, Alpine, and Nordoid elements are also of lower numerical ratio for females. In a paper on taxonomic analysis it is always decisive to include photographs in the proper number.

I first noticed the existence of the Pamirian race in the conquering ancient Hungarians (Magyars) in the small series of Rád (1953b). Later characterized the Turanid type from the morpho-taxonomical point of view on the basis of concrete metrical material concerning males and females (LIPTÁK, 1954a). In the same work I succeeded in outlining the Pamirian type better and in giving its differential diagnosis compared to the Dinaric and Armenoid races.

Also elaborated were the data recorded in the investigations and diary by JÁNOS JANKÓ on the Ostyaks (Khantis) at the end of the last century. I could therefore perform the taxonomical evaluation of the Uralian race of Europeo-Mongolid character

Table 1. Kérpusztá, 11th century (LIPTÁK, 1953).
Taxon means. Males

Measurement number (Martin)	Measurements indices	Gracile Mediterranean (m)		Cromagnoid-A (crA)		Cromagnoid-B (crB)		Dinaric (d)	
		N	M	N	M	N	M	N	M
1.	Glabello-occipital length	22	182,3	17	187,2	16	181,3	12	178,7
8.	Maximum breadth of cranium	23	136,7	18	144,	15	145,1	12	146,2
9.	Minimum frontal breadth	23	97,3	17	101,1	16	100,0	12	98,3
17.	Basion-bregma height	22	133,4	17	138,2	13	135,4	12	138,7
38.	Cranial capacity	22	1370,2	15	1528,5	13	1495,9	12	1515,8
45.	Bizygomatic breadth.	21	129,3	17	137,0	13	133,5	9	138,3
47.	Face height	20	116,6	16	115,3	12	111,6	10	117,2
48.	Upper face height ...	21	68,9	14	69,1	13	66,8	9	71,1
72.	Total facial angle ...	17	87,9°	10	85,8°	9	86,2°	6	86,8°
8:1	Cranial index	22	74,9	17	77,4	15	79,9	12	81,8
17:1	Length-height index .	21	73,0	15	73,7	13	74,5	12	78,4
17:8	Breadth-height index	22	97,7	17	95,2	13	93,6	12	94,9
9:8	Fronto-parietal index	23	71,1	16	70,2	15	68,8	12	67,3
47:45	Facial index	18	91,3	15	84,2	11	86,3	7	84,0
48:45	Upper facial index ..	19	54,0	13	51,1	12	50,4	6	50,5
52:51	Orbital index	22	85,3	15	81,3	14	77,7	12	83,5
54:55	Nasal index	21	47,7	15	52,6	11	53,2	10	46,7
	Calculated stature ...	21	163,1	16	169,0	16	161,4	12	168,5

(1954c). In the analysis of the two large Avar-age series from Üllő (LIPTÁK, 1955a) and the recognition of the Avar-age Mongolids, mainly the Sinid type of females, made this possible.

It became necessary to elucidate clearly and unequivocally the taxonomical position of both the Turanids with Europo-Mongolid character, and the Pamirian race, with respect to both the cranial material and the living population. I did, this in a systematics paper (1955b). The race SCHWIDETZKY (1950) called Turanid is known in the anthropological literature as the Pamirian race. In the same work the metrical and morpho-taxonomical characterization of the Turanid and Pamirian types (Table 3) of the conquering Hungarians was given.

I carried out a comparative analysis in a major monograph on the recent taxon mean-values of Avars and Hungarians in the Danube—Tisza Interstream Region, concerning the Nordoid males and females, as well as the males of Cromagnoid-A type (1957b).

The Avars getting to the Carpathian Basin from Central Asia brought about the „most Mongolid age“ of the Carpathian Basin from century 6 to century 9 when the Mongolid and Mongoloid components amounted together to 16 to 17 per cent of the population. In studying the Mongolid component of the Avars in Hungary, I also established the *differential diagnosis of the Europid and Mongolid great races* and the taxonomical distribution of Mongolids (1959). In this work some taxon

Table 2. Kérpusztá, 11th century (LIPTÁK, 1953).
Taxon means. Females

Measurement number (Martin)	Measurements, indices	Gracile Mediterranean (m)		Cromagnoid-B (crB)		Cromagnoid-A (crA)	
		N	M	N	M	N	M
1.	Glabello-occipital length	23	176,1	12	174,6	10	182,0
8.	Maximum breadth of cranium	23	132,4	11	139,4	9	143,7
9.	Minimum frontal breadth	21	92,3	12	96,1	10	98,5
17.	Basion-bregma height	20	129,6	11	129,6	6	135,0
38.	Cranial capacity	18	1270,2	11	1339,1	6	1404,0
45.	Bizygomatic breadth	20	120,8	11	127,1	8	130,8
47.	Face height	22	109,4	11	103,2	8	112,1
48.	Upper face height	22	64,3	10	61,8	8	66,0
72.	Total facial angle	15	84,4°	9	85,9°	2	89,0°
8:1	Cranial index	23	75,3	12	79,8	9	78,3
17:1	Length-height index	20	74,3	11	74,3	6	75,1
17:8	Breadth-height index	20	98,0	11	93,3	6	95,5
9:8	Fronto-parietal index	21	69,9	12	69,1	9	68,9
47:45	Facial index	19	88,7	10	81,3	6	83,8
48:45	Upper facial index	19	53,5	9	49,2	6	50,1
52:51	Orbital index	22	84,9	12	83,8	9	86,4
54:55	Nasal index	21	49,7	11	57,4	6	53,7
	Calculated statura	21	152,3	11	152,7	9	157,0

Table 3. Ancient Hungarians (10th century)
Taxon means (LIPTÁK, 1955).

Measurement number (Martin)	Measurements, indices	Turanid (t)				Pamirian (p)	
		Males		Females		Males	
		N	M	N	M	N	M
1.	Glabello-occipital length	7	177,8	10	173,6	13	179,1
8.	Max. breadth of cranium	7	150,2	10	145,3	13	153,6
9.	Min. frontal breadth	7	100,7	10	94,3	13	98,6
17.	Basion-bregma height	7	136,0	8	128,6	8	138,0
45.	Bizygomatic breadth	7	139,4	10	131,2	12	138,4
47.	Face height	6	118,5	8	109,8	12	122,7
48.	Upper face height	6	72,8	10	68,6	10	72,5
72.	Total facial angle	4	85,5°	7	85,8°	6	83,8°
8:1	Cranial index	7	84,5	10	83,7	13	85,8
17:1	Length-height index	7	76,2	8	73,8	8	76,8
17:8	Breadth-height index	7	90,3	8	89,2	8	90,3
9:8	Fronto-parietal index	7	66,9	10	65,6	13	64,2
47:45	Facial index	6	85,0	8	84,2	11	88,5
48:45	Upper facial index	6	52,1	10	52,1	13	52,4
52:51	Orbital index	7	82,3	10	83,1	13	82,7
54:55	Nasal index	6	46,6	10	50,3	13	48,3
	Calculated stature	—	—	3	155,6	7	167,7

mean-values were published concerning the following Mongolids: Sinid males (s), Baikal (b) race (males and females), Sajan (sa), or low-faced Mongolid (males and females) and finally the Europeo-Mongolid Jenisej (j), resp. Americanoid taxons (males and females); the Central-Asiatic Mongolid type (ca) was also mentioned but — owing to the small sample size — the taxon mean-values could not be calculated. I called particular attention to the phylogenetic importance of the Bajkal race (1972) and to the fact that this taxon raises the possibility of the Mongolid great race developing from populations of Neanderthaloid type. This idea was raised in the Hungarian anthropological literature first by BARTUCZ (1929) and LIPTÁK (1961).

In our work we established taxon mean-values (Table 4) for the Central-Asiatic (ca) type within the Mongolid great-race (LIPTÁK—MARCSIK, 1976). The Sinid male taxon mean-values could now be calculated on the basis of a larger sample size. The data of the females of Sinid type — on the basis of Üllő I. that quoted earlier — also have a part in this monograph in Table 5.

In the works published later some recent taxon mean-values concerning further Europid races were reported. Enumerated some of these are: Avar-age males of Nordoid type: Homokmégy-Halom (LIPTÁK, 1957a); Alattyán (LIPTÁK, 1963a); Szeged-Kundomb (LIPTÁK—MARCSIK, 1966). — Avar-age females of Pamirian type: Alattyán (LIPTÁK, 1963a); Szeged-Kundomb (LIPTÁK—MARCSIK, 1966).

It has been emphasized that morpho-taxonomical investigation is based decisively upon the principle of taxonomic relevance in selection of characters. The otherwise objective procedure of the so-called „numerical taxonomy“ that does not

Table 4. Avars in Hungary
Central Asiatic (ca). Taxon means (LIPTÁK—MARCSIK, 1976).

Measurement number (Martin)	Measurements, indices	Males		Females	
		N	M	N	M
1.	Glabello-occipital length	7	181,4	9	175,4
8.	Maximum breadth of cranium	7	149,4	9	145,7
9.	Minimum frontal breadth	7	95,0	9	94,1
17.	Basion-bregma height	7	134,2	7	120,5
38.	Cranial capacity	5	1415,6	6	1350,8
45.	Bizygomatic breadth	7	140,5	7	131,1
47.	Face height	6	131,8	8	119,1
48.	Upper face height	7	81,4	9	72,2
72.	Total facial angle	5	85,0°	6	86,3°
8:1	Cranial index	7	82,3	9	83,7
17:1	Length-height index	7	73,6	7	68,3
17:8	Breadth-height index	7	89,9	7	82,9
9:8	Fronto-parietal index	6	63,2	9	64,7
47:45	Facial index	6	94,4	6	91,8
48:45	Upper facial index	7	57,8	7	55,9
52:51	Orbital index	7	82,8	9	88,7
54:55	Nasal index	7	48,5	8	52,4
	Calculated stature	4	166	4	159

differentiate between the taxonomical characteristics seems therefore to be unacceptable. That goes for some statistical procedures, as well.

According the opinion of the author in palaeoanthropological research the points of view of evolutionary taxonomy are uniformly valid. This statement applies with equal force to the process of hominid evolution and to the taxonomy of the subspecies of *Homo erectus* and *Homo sapiens*. There may be some research workers that do regard as dispensable taxonomical research in palaeoanthropological investigation as an aim; the taxonomical method, however, as a means, has verifiably proved to be very useful for revealing the course of microevolution and ethnogenesis.

Table 5. Avars in Hungary.
Taxon means

Measurement number (Martin)	Measurements indices	Sinid (s)				Baikal (b)			
		Males (Lipták—Marcsik 1976)		Females (Lipták 1955)		Males (Lipták 1959)		Females (Lipták 1959)	
		N	M	N	M	N	M	N	M
1.	Glabello-occipital length	5	180,2	15	174,6	12	188,6	7	178,7
8.	Max. breadth of cranium	5	140,0	16	139,8	13	144,4	8	139,7
9.	Min. frontal breadth	4	97,5	17	92,5	13	93,5	9	92,1
17.	Basion-bregma height	5	129,4	7	125,4	11	127,2	8	123,8
38.	Cranial capacity ..	5	1339,4	7	1273,0	8	1403,0	6	1244,3
45.	Bizygomatic breadth	5	136,2	17	126,0	13	136,7	8	125,6
47.	Face height	5	130,2	15	113,0	12	127,3	6	120,5
48.	Upper face height	5	80,8	16	69,7	13	77,2	9	74,0
72.	Total facial angle	5	88,6°	7	84,0°	7	85,1	2	85,0°
8:1	Cranial index	5	77,7	15	80,1	11	75,8	7	77,7
17:1	Length-height index	5	71,8	7	71,9	11	67,6	7	69,1
7:8	Breadth-height index	5	92,3	7	88,8	11	88,7	8	89,4
9:8	Fronto-pariet. index	4	68,6	16	66,0	13	65,0	8	66,1
47:45	Facial index	5	95,6	15	89,3	11	93,1	6	96,8
48:45	Upper facial index	5	59,3	16	54,8	12	56,2	8	58,9
52:51	Orbital index	5	88,7	16	87,4	14	83,9	9	86,1
54:55	Nasal index	5	45,2	15	51,1	13	46,8	7	51,2
	Calculated stature	5	169,0	10	154,9	3	162,0	—	—

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